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The insects comprising the Order Raphidiodea, popularly known as snake-flies, are among the most peculiar of the Neuropteroids. As an ancient group they have retained certain generalized structural features and combined with them various specializations not common to the true Neuroptera. Their interesting and distinctive characteristics have caused them to be the subject of several investigations and two extensive monographs by European entomologists. But in spite of these studies, the Nearctic species have been unsatisfactorily known. The restricted distribution of the insects in North America and their tendency to be only locally abundant has prevented the accumulation of more than a few specimens in most museums, and the great instability of the more obvious structural characteristics has caused much confusion in the taxonomy of our species.

The present revision is an outgrowth of an attempt to eliminate some of this confusion by a study of the genitalia. It soon became apparent, as this study progressed, that the complicated classification proposed by Navas was not only artificial, but, so far as the Nearctic species were concerned, entirely useless. In order to determine the generic position of the Nearctic species, it has been necessary to consider the systematics of the Raphidiodea as a whole, not only of the Recent species, but of the extinct ones as well.

The literature pertaining to the Nearctic snake-flies is not very extensive. At the time when Schneider's "Monographica" was published (1843), the presence of these insects in the New World was not even suspected, and it was not until nearly twenty years later (1861) that Hagen described the first species. Albarda, whose excellent revision of thirty years later (1891) straightened out the taxonomy of the European species, added a great deal to our knowledge of the Raphidiodea in general; but he was able to examine less than 75 specimens from the Nearctic region. Nathan Banks, who has published intermittently on the Nearctic snake-flies since 1895, has been the chief contributor to our knowledge of these insects; and his collection of type specimens has been invaluable in the present investigation. A series of papers by Navas, including a monograph of the World species (written in the Catalonian language!) has served

to confuse rather than clarify the systematics of the Raphidiodea, especially of the Nearctic species, of which he had only a relatively few specimens.

In the course of the preparation of this revision I have been able to examine over 4,000 specimens of Raphidiodea from the Nearctic regions alone. Aside from the collection at the Museum of Comparative Zoology (which contains the types of Banks' species) and a few specimens collected by me in 1932, this material has been loaned to me by various institutions and collectors, whose coöperation has alone made possible the study of such a large series of specimens. To the following entomologists and the institutions with which they are affiliated, I am greatly indebted for the use of their collections: Mr. E. P. Van Duzee and Dr. E. C. Van Dyke, California Academy of Sciences; Dr. F. E. Lutz, American Museum of Natural History; Dr. Harold Morrison and Mr. A. N. Caudell, United States National Museum; Dr. W. T. M. Forbes, Cornell University; Dr. W. J. Chamberlin, Oregon State College; Dr. L. P. Werhle, University of Arizona; Dr. R. C. Smith, Kansas State College; Mr. C. B. Harbison, San Diego Museum, California; Dr. J. M. McDunnough, Ottawa, Canada; Dr. Walter Horn, Berlin, Germany. Special thanks of all who are interested in the Raphidiodea are due to Mr. E. P. Van Duzee and Dr. Van Dyke, for their great activity in collecting these insects, for they have secured nearly a thousand specimens at more than a hundred localities in California and Oregon. For the loan of fossil members of the order I am indebted to Dr. H. G. Rodeck and Prof. T. D. A. Cockerell, University of Colorado; and Dr. E. M. Kindle, Geological Survey of Canada. As on former occasions, I am grateful to Professor Nathan Banks for much helpful advice and criticism.

Since in the Nearctic region the Order Raphidiodea is confined almost entirely to the area west of the Rocky Mountains, the large series of specimens which has passed through my hands constitutes a fairly complete record of the Nearctic fauna. In the collections which I have examined, California, Oregon, Washington and British Columbia have been very well represented; and Arizona, Utah, Colorado and Idaho satisfactorily so. But specimens from Nevada, Wyoming and New Mexico have been all too few. It is from these three states that additional material is most desired. Only a few specimens have been secured in Montana, but these are concentrated in the extreme western part of the state and probably mark the eastern limit of the Raphidiodea in that part of the country.

The study of the genitalia of this extensive series of specimens has

added several species to the number included in the Nearctic region. Up to the present time only eleven species have been described, not including four synonyms. In the present paper nine new species are added, bringing the total to twenty. It is very probable, also, that a few more species will eventually turn up with additional collecting, especially in Nevada, New Mexico and Wyoming.

As a result of the combination of archaic and specialized characteristics, there has been and still is much difference of opinion regarding the relationships between the snake-flies and the other groups of Neuropteroids, especially as to the rank of the former. Linnaeus, who established the genus Raphidia, of course placed the insects in his large and complex order Neuroptera. As that Linnaean order was subsequently broken up into more orders (Trichoptera, Plecoptera, etc.), the close relationship between Raphidia and Sialis, Corydalus, and Chauliodes was recognized and indicated in the various systems of classification used. Latreille, for example, grouped these four genera in one category which he termed Megaloptera. Since the description of a second genus of snake-flies (Inocellia) by Schneider in 1843, there has been an increasing tendency to separate the snake-flies from Sialis and its close relatives. Thus Burmeister (1835) divided the Planipennia into four families, Sialidæ, Panorpina, Raphidiodea and Megaloptera,[1] giving the snake-flies the same rank as the scorpion-flies and the other groups mentioned. Except for degree of rank and for the names used, this classification of Burmeister's is identical with that given by Handlirsch (1908), who elevated each of these families to orders: Megaloptera, Mecoptera, Raphdioidea, and Neuroptera. At the present time there is no universal agreement on the systematic rank of the snake-fly group. Comstock in all his text-books considered them as constituting merely a family of the Neuroptera (including Megaloptera); whereas Brues and Melander (1932), following Handlirsch, give them ordinal rank (Raphidiodea). An intermediate stand is taken by Imms and by Tillyard, who divide the order Neuroptera into two suborders, Megaloptera and Planipennia, the former consisting of the superfamilies Sialioidea and Raphidioidea.[2] It is thus a matter of indi-

[1] Burmeister's Megaloptera included the Myrmecoleontidæ and Hemerobidæ and hence did not correspond to Latreille's group Megaloptera, which was equal to Burmeister's Sialidæ.

[2] Navas has complicated the question of names by using the ending -optera instead of -odea for the name of the order, on the grounds that the former is more suitable for an order. This argument has no weight since there are

vidual preference whether the snake-flies are regarded as comprising a distinct order, or a suborder or family of the Neuroptera. In this paper I have treated the group as an order, because the geological history of these insects shows that they separated from the Sialidæ and Planipennia as far back as the Permian, and that their subsequent evolution has been very different from that of the other groups of Neuropteroids. Certainly at the present period the snake-flies are more distinct from the latter than the Trichoptera are from the Lepidoptera.

The elevating of the snake-fly group from a family to an order has naturally been accompanied by modifications of the generic classification. This question of genera, although a complex one, requires our examination in order for us to determine the generic position of the Nearctic species. The genus Raphidia was established by Linneaus for the European *ophiopsis*, and it remained the only genus of snake-flies for over a hundred years. In 1843 Schneider erected, for the European *crassicornis*, the subgenus Inocellia, which was finally raised to a genus by Albarda in 1891. In 1913, Navas, although still regarding the snake-flies as constituting a family of Neuroptera, established two tribes, Raphidini and Inocellini, each of which included one genus. The following year (1914) he erected a second genus, Agulla, in the tribe Raphidini for a new species, *bagnalli*,[3] which he subsequently (1918) synonymized with Albarda's *Raphidia assimilis* from Vancouver, B. C. In two papers published in 1915

several well established names of insectan orders which do not have the termination -optera. Stitz (1928) has employed the name Raphidiina for the order, but he gives no reasons for his choice. It seems to me that priority should be given to Burmeister's (1835) name Raphidiodea. This was the term used by Handlirsch (1908), though he spelled it with the dipthong "oi" instead of "o"—Raphidioidea. Since the "-oidea" ending is now consistently employed for superordinal and superfamily names, I have followed Brues and Melander in using Burmeister's original term. Navas and several others, including Schneider, have spelled the generic name Raphidia and its derivatives with an "h" asperate—*Rhaphidia*. This is of course the correct spelling from a viewpoint of etymology, but I have followed the original Linnaean spelling, which has been in more general use.

[3] The type locality of *bagnalli* was originally given by Navas (1914, p. 68) as Oceania—a region in which the snake-flies apparently do not occur; that was Navas' interpretation of the label reading "Vancouver I., Victoria, B. C." In 1918 he pointed out that the locality should have been British Columbia, the species being identical with *assimilis*, the type locality of which was also Vancouver.

he established five new genera, as follows: Raphidini, Lesna (genotype, *R. adanada* Alb.), Puncha (genotype *R. ratzeburgi* Brauer), Raphidilla (genotype *R. xanthostigma* Schneid.); Inocellini, Fibla (genotype, *I. maclachlani* Alb.). Originally he included no Nearctic species in these genera, but subsequently (1918) he placed *bicolor* Alb. (type locality, Colorado) in Raphidilla. The following year (1916), deciding to treat the snake-flies as constituting an order, he elevated his tribes to families, Raphididæ[4] and Inocellidæ, and erected four more genera: in Raphididæ, Glavia (genotype *R. adnixa* Hagen), Subilla (genotype *R. sericea* Alb.), Alena (genotype *R. distincta* Banks); in Inocellini, Negha (genotype *R. inflata* Hagen). In Glavia he placed four Nearctic species in addition to the genotype: *R. astuta* Banks, *R. arizonica* Banks, *R. occulta* Banks and *R. oblita* Hagen; in Alena he put two Nearctic species, the genotype and *R. minuta* Banks; and in Negha, two other Nearctic species, the genotype and *longicornis* Alb. In 1918 Navas added another genus, Erma (genotype *abdita* Navas), to the family Raphidiidæ, placing it in a tribe of its own (Ermini) to separate it from the other genera of the family, all of which he placed in the tribe Raphidini. Finally, the following year (1919) he described another genus of the family Inocelliidæ, Estoca (genotype, *peyerimhoffi* Navas) and erected two tribes in that family also: Fiblini, containing Fibla and Estoca; and Inocellini, including the other genera of the family. To summarize, then, Navas' present classification of the order Raphidiodea is as follows:

Family Raphidiidæ
  Tribe Raphidini
    Genera Raphidia, Agulla, Lesna, Puncha, Raphidilla, Glavia, Subilla, Alena
  Tribe Ermini
    Genus Erma
Family Inocelliidæ
  Tribe Inocellini
    Genera Inocellia, Burcha, Negha.
  Tribe Fiblini
    Genera Fibla, Estoca

The chief weakness in Navas' system of classification lies in the nature of the characteristics which he has used for the separation of the genera; for *almost without exception these are venational features*

[4] These family names should, of course, have been Raphidiidæ and Inocelliidæ.

which consistently vary in the individual specimens, and even in the right and left wings of the same specimen. Over ten years ago Banks (1922) published an account of the variation of the venation in the Raphidiidæ, showing conclusively the instability of the characteristics used by Navas. It is not necessary to repeat here in detail the observations by Banks on this question, since the subject of variation of the venation will be considered below more fully. The variations of the wing structure used by Navas are so obvious that it is difficult to understand how he overlooked them.[5] What is even more incomprehensible is that even after the publication of Banks' paper (1922) Navas has continued to use the same characteristics for his genera (*e.g.*, Navas, 1934). Yet a simple computation of the various possible combinations of the characteristics used by Navas shows that a total of *at least* 96 genera can be formed![6]

The latest publication dealing with the classification of the snake-flies is that of Lestage (1928), who apparently being unaware of Banks' paper (1922) already mentioned, concluded from his own observations that Navas' classification was based on characteristics which were secondary on the one hand and too variable on the other. Lestage regards the snake-flies as constituting an order (Raphidioidea) which he divides into three families: Raphidiidæ, having ocelli present, and the pterostigma traversed or at least bordered by branches of Rs; Ermidæ, having no ocelli, but the pterostigma traversed or bordered by branches of Rs; and Inocellidæ, having no ocelli and no pterostigmal branches of Rs. The family Ermidæ includes only the monospecific genus Erma. The other two families are divided into genera on the basis of the presence or absence of the so-called "recurrent vein" in the hind wing, which Lestage identifies as the cross-vein r-m of Comstock (1918, p. 167). The family Raphidiidæ thus consists

[5] Lestage (1928) has pointed out, for example, that although Raphidilla is characterized by Navas as having only one discal cell, Navas' own figure of *Raphidilla formosana* (1918, p. 84) shows two such cells. Similarly, according to Lestage, the species which Navas described as *Inocellia seurati* is a Fibline on one side and an Inocelline on the other!

[6] This figure is of course obtained by multiplying together the numbers of different variations in each structure used by Navas as bases of genera. For example, since he uses the presence of either one or two stigmal veinlets or the absence of all veinlets as generic characteristics, the stigma has a factor of 3. Also, since he employs the presence of one or two radial cells as generic features, this has a factor of 2. Similarly, the discal cells furnish a factor of 2; the branches of the radial sector, 2; and the so-called recurrent vein of the hind wing, 2.

of the subfamily Raphidiinæ in which the recurrent vein is present; and the Raphidillinæ, in which it is absent. The family Inocellidæ includes the genus Fibla, with the recurrent vein present; and Inocellia, with it absent. Lestage's complete classification is therefore as follows:

Family Raphidiidæ
  Subfamily Raphidiinæ
    Genus Raphidia (synonyms: Subilla, Alena, Lesna in part)
  Subfamily Raphidillinæ
    Genus Raphidilla (synonyms: Puncha, Lesna in part), Glavia, Agulla
Family Ermidæ
    Genus Erma
Family Inocelliidæ
    Genus Inocellia (synonyms: Negha, Estoca), Fibla (synonym: Burcha)

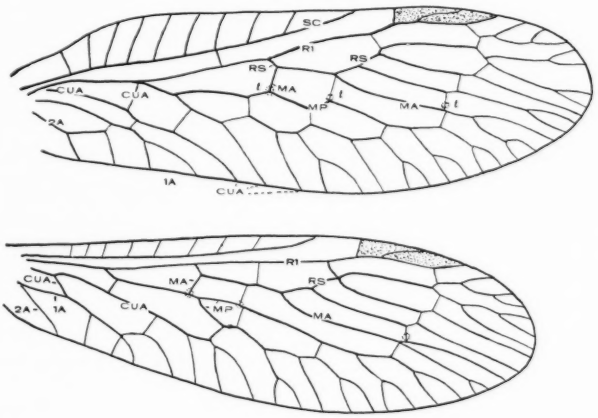
It is apparent that although Lestage has synonymized many of Navas' genera, he has retained certain others: Erma, Glavia, Agulla, Raphidilla, and Fibla. Of these five genera, Erma occupies a unique position; it is a monospecific genus, known only from a single species which is in every respect a perfect Raphidia except that it lacks ocelli. There seems to be a very good chance, especially in view of the high degree of variability of the body structure of the Raphidiidæ as a whole, that the absence of ocelli in this specimen is simply an individual malformation; but even if this is not the case, I do not consider it necessary to establish a separate family *solely* on the lack of ocelli. There are many striking differences between the members of the families Raphidiidæ and Inocelliidæ in addition to the absence or presence of ocelli, and it seems hardly justifiable to erect a family for Erma inasmuch as otherwise it is a typical Raphidia. In treating Raphidilla, Glavia and Agulla as distinct genera, Lestage has unfortunately been lead astray by lack of sufficient material belonging to the two latter genera, which contain American species only. Agulla is monospecific, including the Nearctic *assimilis* Alb.; and Glavia contains the Nearctic species *astuta* Banks, *arizonica* Banks, *occulta* Banks and *oblita* Hagen. The genus Raphidilla, although mainly composed of European species, includes also the Nearctic *bicolor* Hagen. In separating these three genera Lestage simply adopted the venational characteristics used by Navas, obviously because he lacked sufficient Nearctic specimens to enable him to draw his own conclusions. Thus Raphidilla is characterized by having only two

branches of Rs instead of three as in Glavia and Agulla; and the latter two genera are separated by the arrangement of the three branches of Rs; R4 and R5 being fused in Glavia, and R2 and R3 being fused in Agulla. An examination of even a small series of specimens of *assimilis*, however, at once reveals that the arrangement of the branches of Rs varies greatly in the right and left wings of the same specimen. In at least half of the specimens R2 and R3 or R4 and R5 are fused in one wing, although they are not fused in the corresponding wing of the same individual. The distinction between these two genera simply does not exist, and Glavia (Navas, 1916) consequently becomes a synonym of Agulla (1914). In like manner, the venational differences between Raphidilla and the species of Agulla (including Glavia) fail to withstand careful examination. In fully half of the specimens of Agulla, Rs is 2-branched in one wing, and 3-branched in the corresponding wing of the same insect. The individual variation of this particular feature is especially well shown by the fact that Navas placed *bicolor* Alb. in Raphidilla, and *occulta* Banks in Glavia, although as a matter of fact these two species are synonymous! It therefore becomes obvious that the genus Agulla is identical with Raphidilla (1915), the name Agulla (1914) having priority. These modifications in Lestage's classification result in the division of the family Raphidiidæ into two genera, Raphidia and Agulla; and, as was the opinion of Lestage in the case of the Inocelliidæ, it is my belief that there is no need to separate these two genera by subfamilies.

As I have already pointed, out the classification of Lestage rests upon two sets of characteristics,—the absence or presence of the ocelli, and the absence or presence of the recurrent vein in the hind wing. The former feature—the absence or presence of ocelli—provides a satisfactory taxonomic division, since it undoubtedly expresses one of the main divergences in the evolution of the Raphidiodea.[7] But the value of the presence or absence of the so-called recurrent vein as a generic characteristic is sufficiently uncertain to require further examination and study. There is first of all the question whether or not the structure of this vein is constant enough in the individuals to be of generic or even specific use; and secondly the question whether such a characteristic warrants the splitting up of the original genus Raphidia, as it was treated by Albarda.

[7] This is not, of course, true in the case of Erma (even if the absence of ocelli is not a mere malformation), since no other structural changes accompanied the loss of ocelli.

Before taking up these questions, however, it is necessary for us to consider the nature of this so-called recurrent vein or *r-m*, since there already exists some difference of opinion regarding its identity. In certain of the Raphidiidæ and Inocelliidæ the proximal part of the radial sector of the hind wing is connected to the media below it by a short vein (text-fig. 1) which is approximately at right angles to the connected veins and which has all the other appearances of being a true cross-vein (as in *assimilis*). In some other members of both of these

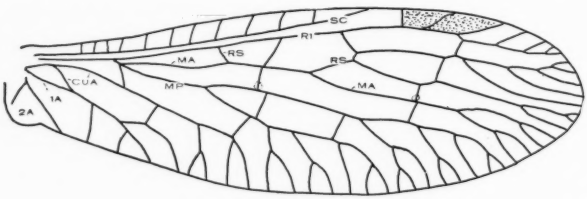


TEXT-FIGURE 1. Fore and hind wings of *Agulla assimilis* (Alb.). Sc, subcosta; Rl, radius; Rs, radial sector; MA, anterior media; MP, posterior media; CuA, anterior cubitus; 1A, 2A, first and second anals; *t*, thyridium.

families (text-fig. 2) the proximal part of the radial sector is connected to the media by a long vein, running parallel to the longitudinal axis of the wing (as in *ophiopsis*); in this case, of course, the vein joins the media at a point close to the origin of the latter. Navas, following Albarda, has termed this long connecting vein a recurrent vein, assuming that it was a secondary vein produced by the backward prolongation of a branch from the radial sector. Lestage, however, following Comstock (1918), identifies the long connecting vein with the apparent cross-vein in the *assimilis* type of wing, designating them both as the radio-medial cross-vein (*r-m*). In this case, of course, the condition in *ophiopsis*, in which the connecting vein is long, is

regarded as a specialization formed by the proximal migration of the point of attachment of *r-m* to the media. Now it is a particularly striking fact that the long form of this so-called cross-vein not only occurs in some members of both the Raphidiidæ and Inocelliidæ, but exists also in several of the families of true Neuroptera (*e.g.*, Hemerobiidæ, Ithonidæ, Sisyridæ, Sympherobiidæ). Since the cross-vein *r-m* does not assume a similar development in any other group of insects, some doubts naturally arise that this long connecting vein really is a modification of *r-m* or even a secondary recurrent vein arising from the radial sector.

The correct homology of this connecting vein in all the Neuropteroids has already been described by Martynov (1928). A study of a series of Permian Neuropteroids reveals that the long vein connecting



TEXT-FIGURE 2. Hind wing of *Raphidia ophiopsis* Linn. (Europe); lettering as in text-figure 1.

the base of the media to the proximal part of the radial sector is in reality a branch of the media, which coalesces with Rs for a short distance and then becomes an independent vein again, forming what appears to be a true branch of the media. In certain of the existing Neuropteroids, as *Raphidia ophiopsis* (text-fig. 2), this coalescence with Rs is still clearly indicated; but in others, as *Agulla assimilis* (text-fig. 1), the proximal part of this front branch of the media has assumed the position of a cross-vein, so that its real nature is not very apparent. Martynov contends, and I believe rightly, that the anterior branch of M which coalesces with Rs is in reality the true anterior media (MA) of Lameere's system of nomenclature, and the rest of the media, the posterior media (MP). Tillyard, who originally regarded the long connecting vein as a modified remnant of the proximal part of the stem of Rs, has subsequently (1932) accepted Martynov's interpretation of this vein in all the Neuropteroids, except that he is not entirely convinced that the anterior branch of M which coalesces

with Rs is necessarily the MA of Lameere. In this paper I have accepted Martynov's interpretation in its entirety, designating the branch of M which coalesces with Rs as MA, and the rest of the media as MP.

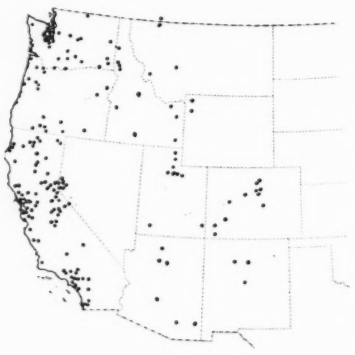
Returning now to the first of the questions raised above, i.e., whether or not the vein connecting Rs and M in the hind wing of the snake-flies is a constant specific characteristic, we now see that we are dealing not with a cross-vein, but with a part of one of the main longitudinal veins. It is not surprising, therefore, to find that whereas the true cross-veins are exceedingly variable in their positions and arrangements, this vein, the free proximal part of MA, is perfectly constant in the species concerned. An examination of the wings of the several thousand specimens of Nearctic species which have passed through my hands shows that invariably in all of these species MA is formed as in *assimilis*. A similar study of the European species[8] reveals that although some species (as *nigricollis*) invariably have the free proximal part of MA formed as in the Nearctic ones, others (as *ophiopsis*) always have this part of MA very long, the vein originating at the base of M. It is clear then that the free proximal part of MA is a stable feature, and since the two forms of the vein occur in both the Raphidiidæ and Inocelliidæ, it provides a very satisfactory means of grouping the species of each family.

The question whether these groupings are to be regarded as of generic or subgeneric value depends to a large extent upon personal preference, but I believe that the geological and geographical distribution of these groups supports the policy of recognizing them as genera, as was done by Lestage. This view is also upheld by a study of the male genitalia, since a comparison of the genitalia of the species of Agulla and Fibla shows that their structure is very different from that in the genera Raphidia and Inocellia, respectively. As treated in this paper, therefore, the order Raphidiodea consists of two families: Raphidiidæ, with the genera Raphidia, Agulla, and Erma; and Inocelliidæ, with the genera Inocellia and Fibla.

The geographical distribution of the snake-flies is particularly interesting since it conforms to that frequently found in groups of animals and plants which are geologically old. Only two of the above genera, Agulla and Inocellia, are represented in the existing North American fauna, however. Raphidia, as characterized above, occurs

[8] In this connection I am under obligation to Mr. F. J. Killington, who kindly examined for me a series of European species in his collection and that of the University of Oxford Museum.

in Europe and Asia; Erma only in Northeastern Spain; and Fibla in southern Europe. Agulla, the most widely distributed genus, inhabits not only part of North America, but also Chile, Central America, and part of Asia; and Inocellia occurs in Central Europe, Asia, and northern Africa, as well as part of North America. It is apparent, then, that with the exception of the single Chilean species, *Agulla herbsti* (Peters.), the Raphidiodea are confined to the Northern Hemisphere, and that fully ninety-five per cent of the species inhabit only the Holarctic regions. No snake-flies have yet been found in the Australian or Ethiopian regions, and it is extremely doubtful



TEXT-FIGURE 3. Distribution of the Raphidiodea in the United States.

that any native species will ever be secured there.[9] In the Nearctic region the insects are confined to the area west of the eastern slopes of the Rocky Mts., extending northward into the southern part of British Columbia, as far as latitude 52°. In view of the wide distribution of the snake-flies in Europe, their absence from the eastern half of North America is particularly striking and has some bearing on the question of the origin of the Nearctic species, as I shall show later. In all probability the eastward migration of these insects has been prevented by the extensive arid areas just east of the Rocky Moun-

[9] In 1890 and again in 1891 attempts were made for economic reasons to introduce "a common Raphidia" into New Zealand from California. Probably several species were included in the shipments; at any rate the insects failed to become established. See Insect Life, Vol. 3, 1891; p. 43; and also Vol. 4, 1892; p. 339.

tains. Since the snake-flies pass through their immature stages under the bark of pine, fir, Eucalyptus, and related trees, they are always absent from regions which are too arid for these trees. In view of the poor flying capacity of these insects, their occurrence in pine forests on the peaks of the "island" mountain ranges of the desert of Arizona is therefore more than a little remarkable.

The two families of Raphidiodea which occur in the Nearctic region are not equally distributed in that area. The Raphidiidæ have the greater range, including the entire Californian and most of the Rocky Mountain regions, as defined by Wallace; the Inocelliidæ, on the other hand, have only been found (so far as I am aware) in the Californian region.

Although there are many other structural differences between the Raphidiidæ and the Inocelliidæ, the characteristics given in the following key will enable easy recognition:

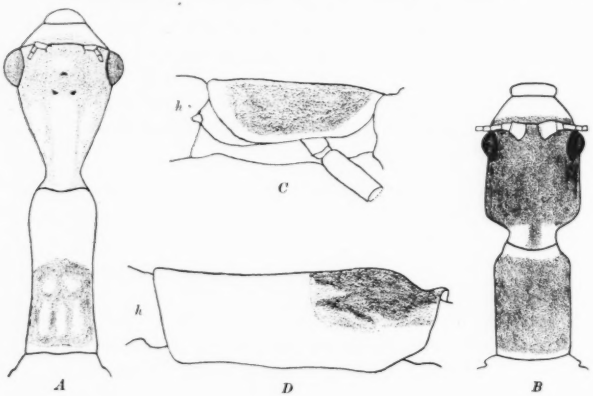
Ocelli present; pterostigma bordered proximally by a veinlet from R1 ..... *Raphidiidæ.*

Ocelli absent; pterostigma not bordered proximally by a veinlet ..... *Inocelliidæ.*

Family Raphidiidæ

Head longer than wide, usually narrower posteriorly than anteriorly; antennæ remotely inserted, with about thirty-five segments, the first segment only about twice as long as the second; clypeus large, very wide; maxillary palpi 4-segmented; labial palpi 3-segmented; mandibles small, with three or four teeth; eyes prominent, situated on the sides of the head, almost contiguous with the clypeal margin; ocelli present. Prothorax long and slender, usually at least as long as the rest of the thorax; pronotum expanded laterally and ventrally, forming a collar which envelops the whole prothorax (text-fig. 4); meso- and metathoracic segments short, not so long as wide; prothoracic legs attached to the posterior part of that segment, 3d tarsal segment enlarged and flattened, the 4th very small. Male abdomen usually terminating dorsally in a hood-shaped epiproct; male genitalia differently formed in the several genera, but always enclosed laterally and sometimes ventrally by a pair of harpogones; female abdomen terminating dorsally in an epiproct like that of the male; ovipositor about as long as the entire thorax, usually sickle-shaped. Fore wing: costal margin arched, the costal space broadened to a variable degree and containing a series of veinlets, the number differing in individuals; Sc terminating beyond the middle line of the wing; R1 without true branches, although giving rise to several cross-veins which border

and frequently traverse the pterostigma; Rs arising at about the middle of the wing, forming at least two main branches (R2 + 3, R4 + 5), which are usually subdivided and twigged; M divides into MA and MP at about the middle of the wing; MA directed anteriorly immediately after its origin, in the form of a cross-vein, and coalescing for a short distance with Rs, before continuing as a free vein; MP dividing into two main branches proximal of the origin of MA[10]; both these branches of MP are subdivided and the posterior branch coalesces



TEXT-FIGURE 4. Head and prothorax of *Agulla adnixa* Hagen (A, D) and *Inocellia inflata* Hagen (B, C). A and B, dorsal views; C and D, lateral views; h, head.

for a short distance with CuA; CuA divided proximally into a short posterior branch and a long anterior one, which coalesces with the stem of M for a short distance, and then forks, the anterior fork coalescing with MP for a short distance; CuP absent; both 1A and 2A are forked. The hind wing is a little shorter and more slender than the fore wing and the costal space is uniformly narrow, but in most respects the venation is the same. Rs arises closer to the base of the wing than

[10] The fact that MA arises *after* the division of MP seems at first glance to suggest that the former is not in reality the anterior media of Lameere's nomenclature; but the structure of this vein in the hind wing indicates that there has been a distal migration of the point of origin of MA, from the base of M to near the mid-wing.

in the fore wing, and MA originates either as in the fore wing or arises from the base of M; CuA divides close to the base of the wing; the anterior branch is entirely free from M and MP, but the posterior branch coalesces for a short distance with 1A; 1A is unbranched, 2A forked. From two to four thyridia are present on both fore and hind wings.

Very little is known of the internal anatomy of the Raphidiidæ. The only general account was published nearly ninety years ago by Loew, who discussed and figured unusually well the gross internal morphology of *Raphidia ophiopsis* Linn. How different the internal anatomy may be in other snake-flies is not of course clear, but in that species the structure is most unusual. The salivary glands consist of a pair of very long tubes, extending more than half the length of the whole body. There is a very large, cordate food-sac, attached to the posterior part of the crop, which is of course very long as a result of the tenuate prothorax. The mid-intestine is large, and the Malpighian tubes, which are six in number, are well developed. The latter are particularly interesting since (according to Loew) four of the tubes are attached at their tips to the colon. The other structures are not so unusual as the alimentary tract, but it is very desirable that additional studies be made upon the internal anatomy of these insects.

Almost nothing is known of the life-history and general biology of the Nearctic snake-flies. Kellog includes figures of a larva and pupa in his "American Insects," presumably of an American species; but so far as I am aware nothing whatever has been published on the biology of the Nearctic Raphidiodea. In 1927 I was able to make a few observations on the habits of the adults and larvæ of *Agulla unicolor*, n. sp., in California, though I had no opportunity of studying the life-history. The life-history of the European Raphidiidæ, however, has been at least partially known since the time of Linnaeus, who was himself acquainted with the pupa. At about the beginning of the nineteenth century Walckenaer succeeded in rearing these insects, and published the first accurate account (1802) of their life-history. Schummel (1832), Percheron (1833), Waterhouse (1834), and Schneider (1843) contributed further details on the biology of the European snake-flies; and in recent years interesting accounts have been given by Campion (1915), Lucas (1928), Williams (1913), Lyle (1913), Morley (1909), Killington (1931), and others. It is indeed fortunate that these European entomologists have given so much attention to the development and habits of these insects; and it is with the hope of stimulating interest in the biology of the Nearctic

species that I include here the more important observations on the habits and life-history of the European Raphidiidæ.

The adults, though properly classed as predatory insects, are capable of catching and killing only small and very weak prey. Campion (1915), who kept several adults of *Raphidia notata* in captivity for over a month, provided them with small Diptera, but noted that the snake-flies were very reluctant to attack them. He obtained better results by giving them injured flies and aphids, which were seized and readily eaten. Williams (1913), however, succeeded in feeding the snake-flies daily with living aphids. "The aphis was approached slowly and cautiously at first, then captured by a sudden rush and raised aloft in the jaws, the long prothorax of the snake-fly being elevated in the manner characteristic of these insects. The prey was then slowly but completely consumed, the legs and antennæ, which usually stuck on the head of the Raphidia being cleaned off by drawing the tarsus over the top of the head. The pieces were in this way transferred to the tarsus, which was then drawn downwards between the mandibles and the last remnants were removed and eaten-up." On this diet Williams was able to keep one female alive for the surprisingly long period of 68 days,—a longevity which is unusual for the Neuropteroids. In 1927 I found that *A. unicolor*, n. sp., would feed readily on freshly killed Chironomidæ, even comparatively large species. The females, as Williams also noted, have a curious habit of frequently wagging their ovipositor during the process of eating, as though expressing satisfaction with the food. The adults make very thorough attempts to clean up after each meal. The head and mandibles are easily cleaned as described above, but the hind legs offer some difficulty. One female of *A. unicolor* which I observed in 1927 spent fully a half hour scraping and wiping the hind legs with the others and against various parts of the body in an attempt to remove some small remnants of the body fluid of a recent victim. The antennæ are cleaned by drawing them through the fore tarsi.

Although the observations on the feeding habits give the impression that the adults are not by any means vicious, it is apparent that they readily become cannabalistic. Williams (1913) placed two females of *A. maculicollis* in a single container and found in the course of an hour or two that one specimen had chewed the head off the other and consumed its abdomen. Similarly, Lyle (1913) put about two dozen specimens in three large pill boxes, and discovered one or two hours later that most of these had been reduced to a pile of legs, antennæ and debris in the bottom of each box, though a few much mutilated specimens were still fighting.

No observations have been made on the mating habits of the snake-flies, which is most regrettable since they are probably unusual. Campion (1915) attempted to bring about the mating of a pair of *R. notata*, but whenever the two specimens confronted each other, both of them manifested great alarm and backed hastily away, the female being the more disturbed.

The eggs of the Raphidiidæ are usually deposited in clusters in crevices of the bark of pines, spruce, holly Eucalyptus and perhaps related trees, although according to Lucas they are sometimes laid on dead wood. The individual eggs are small, less than 1.5 mm. in length, and shaped very much like a banana. The micropyle is in the form of a small cylindrical protuberance.

The larvæ of the Raphidiidæ are robust and very active creatures, with large flat heads and short legs. The mandibles are only of moderate size, and are very similar to those of the adults. The antennæ are setaceous, less than half as long as the head, and 3-segmented (or 4-segmented, if the minute basal piece is included). The eyes, which are small and semi-globular, are arranged in two groups, one just behind each antenna on the sides of the head. A perplexing difference of opinion exists regarding the number of eyes. Latreille (1798) stated that the larva of *R. ophiopsis* possessed only two ocelli on each side of the head, which was confirmed by Waterhouse (1836), and Westwood (1840); but Percheron (1833) gave the number as seven and this was substantiated by Schneider (1843), who was probably more thoroughly acquainted with the immature stages of the snake-flies than any other student of the group. Three larvæ of European species in the Hagen collection at the Museum of Comparative Zoology possess seven ocelli on each side and this is likewise true of the two larvæ which I secured in California in 1927. It is, I think, quite probable that the larvæ with only two ocelli on a side were members of the family Inocelliidæ rather than the Raphidiidæ. Schneider described the larvæ of the Inocelliidæ as having four ocelli on a side, but two of these are so very minute that they might easily have been overlooked by the earlier observers mentioned.[11]

The prothorax is flat, broad, and about as long as the other thoracic

[11] Unfortunately Waterhouse did not indicate the locality at which his larvæ were found. Although he assumed with some doubt that his larva was *R. ophiopsis*, it has more recently been determined that *ophiopsis* does not occur in England, in which Waterhouse presumably lived at the time. The family Inocelliidæ does not occur in England either, but there is some probability that he may have secured the larva on the European continent.

segments combined; the pronotum is enlarged and covers the whole of the prothorax and part of the sides; the abdomen, which is fully as broad as the rest of the body, consists of ten easily distinguished segments. The number of instars of the Raphidiid larvæ has apparently not been determined; at any rate the length of the larval period varies a great deal in the different species. According to Killington (1931) *R. notata* hibernates in the larval stage, and the same is true of *A. xanthostigma* (Syms, 1913). Syms suggests that the metamorphosis of the Raphidiidæ may extend over a two year period, for some larvæ which he kept for a year moulted only three times, and then had not reached the pupal stage.

The larvæ usually live under the bark of the trees mentioned above, although they frequently occur in a variety of other situations. Campion reports (1915) finding two larvæ in some Sphagnum moss which had been thrown upon the ground near a group of Scotch fir; and Lucas discovered one larva in a spruce-fir cone (1928). The latter also noted that the larvæ were consistently abundant in Scotch fir at the bases of branches which had previously been broken away, the remaining part being more or less decayed. The larvæ occasionally make channels in soft rotting wood, as was observed by Campion (1915) and Morley (1909). Although they are predaceous, the larvæ are hardly vicious; their chief source of food in nature seems to be small, helpless insects, such as plant-lice and caterpillars. The only account of which I am aware that attributes voracious feeding habits to the snake-fly larva is in Insect Life (vol. 3, p. 43, 1890), where it is stated that the larvæ attacked and devoured codling moth caterpillars twice their own size. Because of their supposed appetite for codling moth caterpillars, an attempt (which failed) was made to introduce a Californian Raphidiid into New Zealand; and it was also stated that an effort would be made to introduce these "ravenous creatures" into the eastern apple orchards. Specimens in captivity will feed readily on larger insects, such as flies, but these must be injured or entirely killed before the Raphidiid larva will attempt to attack. On one occasion Campion placed a small spider in a box containing a *notata* larva, but the latter showed such great alarm that the spider was removed; the same larvæ, however, readily ate freshly killed spiders. The larvæ have a curious habit of running backwards with great rapidity, and if disturbed jerk their head and open their mandibles in a threatening manner. Although it has been my observation that the larvæ run backwards without any extraordinary manoeuvres, Lucas (1928) states that they do this like a "looping caterpillar."

The last few distal segments of the abdomen possess a slight amount of prehensile power, however, and it is possible that the larvæ can use the end of the abdomen (which is of course devoid of legs) in this way. When it reaches maturity the larva forms a crude, unlined, oval cell in the bark or in partially decayed wood, and pupates in the normal manner.

The pupa is of the *libera* type and is remarkable for its activity. The body structure as a whole is, of course, almost identical with that of the adult, except for the mandibles, which curiously enough are the same as those of the larva. In the female pupa the distal half of the ovipositor is held flat against the dorsum of the abdomen, producing a strong curve in the middle part of the ovipositor, which is not entirely eliminated in the adults. The pupal period is variable in duration. In *R. maculicollis* the pupa is the hibernating stage, extending from October to April; whereas in *R. notata* and *A. xanthostigma* it lasts from two or three weeks (Morley, 1909; Hess, 1923). As the pupa approaches maturity it becomes more and more active. Several days before the adult emerges the pupa is able to bite objects defensively with its mandibles, to grasp objects with its legs, and to move both the head and abdomen freely. About a day before the adult emerges, the pupa bites its way out of the cell and runs actively over the bark of the tree, even up vertical surfaces.

Although the actual emergence of the adult is as rapid as in most other insects, the assumption of the perfect adult form is surprisingly slow, which is probably another indication of the primitive nature of the snake-flies. Morley (1909) observed that the adult of *R. notata* occupied fully six hours in this process of transformation. The wings expanded at the usual rate, but these, as well as the legs, antennæ and various other parts of the body remained a pellucid white for many hours. This slow development explains why so many of the adults which have passed through my hands have possessed this peculiar whitish appearance.

It is interesting that only a single parasitic insect, *Pyracmon melanurus* Holmg., has been bred from the Raphidiidæ. The larva of this parasite issued from the larva of a Raphidia (Williams, 1913), which at the time was the only known host. Lucas (1928) has called attention to the death of one larva from the fungus *Empusa lampyridarum* Rol.

The family Raphidiidæ, as treated in this paper, consists of three genera: Raphidia, Agulla, and Erma. Only one of these, Agulla, is present in the Recent Nearctic fauna or in fact in the entire New World, although Raphidia is represented in the Miocene of Colorado.

Genus *Agulla* Navas

Agulla Navas, 1914, Bol. Soc. Arag. Cienc. Nat., 13: 66.
Puncha Navas, 1915, Mem. R. Acad. Cienc. Art., 11: 396.
Raphidilla Navas, 1915, Mem. R. Acad. Cienc. Art., 11: 477.
Lesna (in part) Navas, 1915, Mem. R. Acad. Cienc. Art., 11: 396.
Glavia Navas, 1916, Mem. R. Acad. Cienc. Art., 12: 509.

Since this is the only extant genus of the family in the Nearctic region, there is no need to discuss further the characteristics of these insects. The differences between Agulla and the Old World genera have already been discussed. The synonymy of the genera erected by Navas has also been considered above with the exception of the genus Alena, which was erected by him to include the two small Nearctic species *minuta* Banks and *distincta* Banks. As pointed out by Lestage the characteristic on which Navas founded this genus (the number of thyridia) is scarcely sufficient to warrant a distinct genus. In *distincta* and *minuta* there are four of these hyaline spots on each wing, as indicated in text-figure 6; in the other Raphidiidæ there are either two or three thyridia, the one just below the pterostigma in *distincta* and *minuta* never being present. But an examination of the male genitalia of the two latter species shows that the male genital structure is very different from that of the other species of Agulla, as mentioned by Banks long before Navas erected Alena. The genitalia of *minuta* and *distincta* are so distinctive that it seems advisable to place these species in a separate subgenus (Alena) of Agulla.

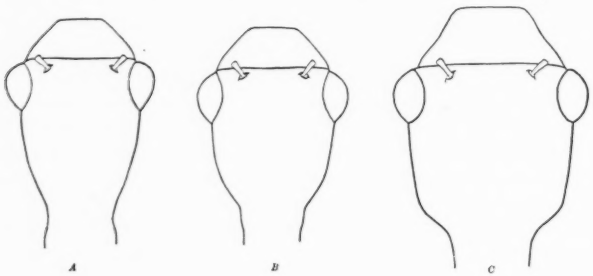
The chief characteristics on which the Nearctic Raphidiidæ have previously been classified are: (1) the color of the body; (2) the shape of the head and thorax; (3) the wing venation and form of the pterostigma; and (4) the general shape of certain terminal abdominal segments, such as the epiproct ("upper appendage"). The present study was undertaken with the hope of finding more satisfactory structural characteristics in the internal genitalia, since these have proved so reliable in the classification of other Neuropteroid insects. It soon became apparent, as the study of the genitalia progressed, that the four groups of characteristics enumerated above are even more unsatisfactory than was suspected, as indicated in the following summary:

1. Color of body. The color of the body as a whole is exceedingly variable in most species, especially in pinned specimens. The color frequently differs in intensity on the two sides of the same specimen, one side being dark brown and the other light brown. The color of

certain portions of the body is also very unstable, including that of the head, a feature which has been consistently used by Navas. The basal color of the top of the head of all Raphidiidæ is reddish black, this surface being minutely punctate. There are certain areas on the top of the head which have a perfectly smooth surface and which are distinctly red in color. The typical pattern in *Agulla assimilis* is shown in text-figure 4, and this same general pattern persists in all the species of the family. Previous students of the snake-flies, Navas in particular, have used the differences in the size of the reddish areas as specific characteristics; but the study of the large series of Agulla which have passed through my hands shows conclusively that the size of the reddish patches varies freely in the individuals of the Nearctic species, and undoubtedly does the same throughout the Raphidiidæ as a whole. There are some species, of course, in which the variation is greater in a certain direction than it is in other species; but to designate one detailed pattern as definite for a given species, as has been done by Navas, is entirely unwarranted. The coloration of the pronotum is a much more useful characteristic than that of the head. In nearly all the species of Agulla, and the Raphidiidæ as a whole, the posterior half of the pronotum contains a large reddish-black patch like the background of the head; the anterior half of the pronotum in most of the species of Agulla is either brown or reddish brown, at any rate much lighter than the posterior half. In a few species, however, the dark patch on the posterior half of the pronotum is consistently absent (*e.g.*, *unicolor*, n. sp.), the pronotum as a whole being therefore of one color. This feature, being readily discernible, is a very convenient one to use. Banks has also noted that the intensity of the color of the first antennal segment with respect to the segments immediately following (*e.g.*, whether darker or lighter) is a useful characteristic. I find that this breaks down only in a very few species. The color of the abdomen appears to be fairly constant in a few species and this is likewise true to an even greater extent of the harpogones.

2. The shape of the head is a characteristic which has been used specifically by all students of the snake-flies since the time of Schneider (1843). The difference in the shape of the head of various specimens is certainly so striking that one is naturally tempted to use this feature specifically. My efforts in this direction were soon ended, however, for it turned out that the shape of the head is another unstable feature, as indicated by the genitalia. A typical case is afforded by *A. arizonicus* (Banks), as shown in text-figure 5; the specimens illustrated were

collected at the same locality, have an identical genital structure, and show no differences except in the shape of the head. There are some species of Agulla which *seem* to have the head broader on the average than others, but these are rare species only, which are not represented by as many specimens as the others. The clypeus varies a great deal in shape, but this also is an individual variation. The relative length of the prothorax is a useful characteristic in distinguishing certain species. The size of the prothorax is best expressed in relation to the height or vertical thickness rather than to the width, which is very unstable.



TEXT-FIGURE 5. *Agulla arizonica* (Banks): variation in the shape of the head.

3. The wing venation has been used chiefly by Navas in the taxonomy of the species. As has been mentioned above, Banks and Lestage have already called attention to the undisputable fact that the venation is extraordinary variable, even in the corresponding wings of the same individual. The shape of the wings, as in the case of other groups of Neuropteroids, is too variable in the individuals to be of specific value; but the width of the costal space seems to vary only within small limits. Certain species (*e.g., A. bifurca* Banks) undoubtedly have a much narrower costal space than others (*e.g., A. bractea*), in which this area is unusually broad. The majority of species, however, have the costal space more or less intermediate between these extremes. The length of the pterostigma in proportion to its width is the most satisfactory of the wing characteristics. Unfortunately the pterostigma is shaped very much the same in most of the species of Agulla, but in a few it is quite unique (*e.g., A. distincta*). The color of the stigma is of very little specific value, this varying as much as that of the body. Albarda established one species, *bicolor*, because the

pterostigma was not of a uniform brown; but as I shall show below the bicolored stigma is merely in individual variation which occurs in all degrees of perfection.

4. The shape of the epiproct ("upper male appendage") in the male, and of the terminal sternites in the female has been used consistently by most students of the Raphidiidæ. So far as Agulla is concerned, the epiproct (which is always hood-shaped) is obviously differently shaped in some species from what it is in others; but most of the peculiarities which have been attributed in the past to the natural form of the epiproct are in reality the result of the shrinking and shriveling of the insect's abdomen after death. The only way to determine the true shape of the epiproct is to soften the end of the abdomen in boiling water and then observe the epiproct after it has been completely relaxed. Generally speaking, however, this is not worth while since the epiproct is practically identical in nearly all species. The last abdominal sternite and tergite in the females of the Nearctic Agulla show absolutely no differences in shape so far as I can discern. Hagen (1867) used the form of these plates to distinguish between certain of the European Raphidia, but there is no such diversity in the structure of the Nearctic Raphidiidæ.

It is the male genitalia which provide us with the most definite and satisfactory means of classifying the species of Agulla. With the exception of a few very brief remarks of Hagen, no attempt has previously been made to treat the snake-flies on the basis of the genital structure. In part as a consequence of this neglect, as well as the peculiarity of the genitalia themselves, the homology of these structures with those in other insects is not at all clear. Crampton (1918) has given an account of this subject, but in this paper I have employed for purposes of convenience the terminology used by Snodgrass (1935). The genitalia of Agulla (*s. str.*) themselves are covered dorsally by the hood-shaped epiproct (ep) previously mentioned, and are confined laterally and partially ventrally by the flat harpogones (hrp), which terminate distally in a long, flat tooth-like process. Of the several structures concealed within the genital chamber the only ones which are strongly chitinous and which concern us as a taxonomic tool are the parameres (pmr), a pair of diversely formed structures which are attached to the ædeagus. There are several distinctly different forms of the parameres. In *A. oblita* (Hagen)[12] they consist of a pair of thick, but sharp hooks (figures 8, 9); in

[12] The specimen which Crampton figures (Psyche, vol. 25, pl. 2, fig. 16) is *oblita*, not *occulta* as named.

several other species they are in the form of a pair of flat or slightly convex plates, the shape of which is in general very constant in any species or at most varies insignificantly. The only exception to this approximate uniformity of structure is found in *unicolor*, n. sp., most specimens of which lack entirely the chitinous parameres; in a few specimens, however, they are represented by a pair of minute flat lobes, and in an even smaller number of specimens the parameres are fully developed, being precisely like the minute ones, except for size. This species seems to be in the process of eliminating the parameres entirely. In most of the species possessing these plate-like parameres, the latter have one or more thick, spiny ridges extending transversely across the plate (*e.g.*, fig. 16). Although there is slight variation in the number and position of these ridges within the species, the variation is never great enough to be confusing, so that such differences as exist between the parameres of *bifurca* Banks (fig. 17) and *occidentis*, n. sp. (fig. 21), for example, are always clear. In a few species the parameres are peculiarly modified into forms much unlike the foregoing; thus in *flexa*, n. sp. (fig. 10), they consist of a pair of very thick, curved hooks, and in *banksi*, n. sp., of a pair of plates with the ridges enlarged into lobes. It is at once obvious, after a survey of the types of parameres illustrated on plates 1 and 2, that with the exception of those of *adnixa* Hagen and *flexa*, n. sp., the parameres are modifications of the same general type; the other parts of the genitalia of the two excepted species, however, are so much like those of the remaining species that there is certainly no occasion for establishing a subgenus for them.

When we examine the genitalia of *distincta* Banks and *minuta* Banks (fig. 6, 7), we find a fundamentally different type of structure: there is an elongate hypandrium, a very distinctive epiproct, and parameres which are not in any way comparable with those of the foregoing species. For this reason I consider *minuta* and *distincta* as comprising a distinct subgenus, *Alena* Navas, to emphasize the difference in their anatomical structure from that of the other species which consequently comprise the subgenus Agulla.

It may be helpful to note that when the specimen has been adequately relaxed, the examination of the genital chamber can be accomplished without any troublesome dissection. Almost always the harpogones are closed in such a way that they conceal the structures within, but these are easily spread apart by hooking the bent tips of a pair of fine insect pins under the inner edges of the harpogones (see figures 2, 3). In this way the parameres can be examined without actual dissection of the parts.

Although we are able to classify the males of Agulla easily and accurately on the basis of the genital structure, I have been utterly unable to find any means of placing the taxonomy of the females on a similar basis. The external genitalia do not present any satisfactory characteristics and there appear to be no chitinous plates internally attached to the 9th sternite, as in the Mecoptera, some Trichoptera and Neuroptera. The females of most of the species can be recognized with a fair degree of certainty, however, by means of the various characteristics mentioned previously (*e.g.*, color of prothorax and antennæ, shape of pterostigma, etc.); but the females of a few species such as *arizonica* and *assimilis* seem to be indistinguishable.

Up to the present time thirteen species of Agulla have been described from the Nearctic region, as follows: *adnixa* Hagen, *oblita* Hagen, *assimilis* Albarda, *bicolor* Albarda, *arizonica* Banks, *crotchi* Banks, *astuta* Banks, *bifurca* Banks, *occulta* Banks, *minuta* Banks, *distincta* Banks, and *bagnalli* Navas. The latter species (based on one specimen) was synonymized by Navas himself with *assimilis* Albarda after discovering that the type locality of his species was British Columbia instead of Oceania. The type of one of Hagen's two species was completely destroyed in 1890 during transit to Albarda, and the type of the other is in the Berlin Museum; but his descriptions are so complete that the identity of his species is certain. The types of Albarda's two species are in the McLachlan collection, and I have not seen them; but as with Hagen's species, their identity is satisfactorily clear. The types of the remaining species, all described by Banks and deposited in the Museum of Comparative Zoology, have of course been studied in connection with this revision.

The following key to the males of the Nearctic species of Agulla is based mainly on the structure of the parameres, though color characteristics have been used whenever reliable. This key expresses to a certain extent the approximate relationship between the species. The key to the females is of course based almost entirely on coloration, and does not therefore express relationships or give as precise determinations as that dealing with the males. In certain cases in which I have been unable to distinguish between the females of certain species, nothing more could be done than simply to designate the species concerned in the hope that collecting data or probable association with males will provide the necessary information needed for further identification.

Key to the Males of Agulla

1. Epiproct (ep, fig. 25) in the form of a curved hood. (Subgenus Agulla) ..... 2.
   Epiproct (ep, fig. 6) in the form of a flat bilobed plate. (Subgenus Alena) ..... 18.
2. Parameres entirely absent; pronotum unicolored ..... *unicolor*, n. sp.
   Parameres present; pronotum either bicolored or unicolored .... 3.
3. Parameres consisting of a pair of large curved teeth (Fig. 8, 9) *adnixa* Hagen.
   Parameres otherwise formed ..... 4.
4. Parameres in the form of a pair of "c"-shaped processes, curved away from each other; harpogones with a prominent lobe below the distal tooth (fig. 10) ..... *flexa*, n. sp.
   Parameres in the form of a pair of flat or nearly flat plates, sometimes curved or lobed ..... 5.
5. Parameres consisting of a pair of flat or nearly flat plates bearing one or more serrated horizontal ridges ..... 6.
   Parameres diversely formed, but not possessing horizontal ridges ..... 13.
6. Parameres obliquely placed with respect to the ædeagus, the upper (distal) end of plates being more remote from each other than the lower ends (fig. 22) ..... *astuta* Banks.
   Parameres placed parallel with the ædeagus ..... 7.
7. Parameres very small, much less than half the length of the harpogones (fig. 2) ..... *neglecta*, n. sp.
   Parameres nearly as long as the harpogones ..... 8.
8. Lower end of parameres abruptly curved outwards at a 90° angle to the rest of the plate; first antennal segment darker than the following segments (fig. 20) ..... *bicolor* Albarda.
   Lower end of parameres straight; first antennal segment not darker than the following segments ..... 9.
9. Parameres very nearly as broad at the lower end as at the middle; only one ridge near the middle part of the plate (fig. 23) *singularis*, n. sp.
   Parameres much narrower at the lower end than at the middle; at least two ridges near the middle portion of the plate ..... 10.
10. Parameres diamond-shaped, with two very prominent ridges (fig. 16) ..... *bractea*, n. sp.
    Parameres elongate-oval, or semi-oval in shape ..... 11.
11. Parameres convex, the middle part bulging out well beyond the level of the margins (fig. 21) ..... *occidentis*, n. sp.
    Parameres flat ..... 12.
12. Parameres containing three prominent, equally spaced ridges, best developed on inner side of plates; prothorax unicolored. (fig. 17) ..... *bifurca* Banks.

Parameres containing three (rarely four) unequally developed and spaced ridges, best developed at the middle of the plates; prothorax bicolored (fig. 18, 19) ..... *assimilis* Albarda.

13. Parameres flat, ribbon-shaped plates, curved outwards at both ends; pronotum bicolored (fig. 14) ..... *arizonica* Banks.
Parameres otherwise formed; pronotum unicolored ..... 14.

14. Parameres curved along a line parallel with the ædeagus (fig. 15) *crotchi* Banks.
Parameres not so curved ..... 15.

15. Parameres with a distinct lobe, arising from the lower end ..... 16.
Parameres without lobes ..... 17.

16. Lobe of parameres long and vertical, about twice as long as wide; apex of plate rounded and only slightly recurved (fig. 13) .. *modesta*, n. sp.
Lobe of parameres short and oblique, not so long as wide; apex pointed and overhanging the rest of the plate by half its length (fig. 11) ..... *banksi*, n. sp.

17. Parameres small, suboval plates, sometimes very minute; pronotum unicolored (fig. 1) ..... *unicolor*, n. sp.
Parameres large, ear-shaped, with a thickened outer margin (fig. 3) ..... *directa*, n. sp.

Key to Females of Agulla

The females of the following species are unknown: *banksi*, n. sp.; *crotchi*, Banks; *directa*, n. sp.; *flexa*, n. sp.; *neglecta*, n. sp.; and *singularis*, n. sp.

1. Very small insects, the length of the fore wing being less than 8 mm.; 4 thyridia present in each wing (text-fig. 6). Subgenus Alena ..... 2.
Small to large insects, the length of the fore wing being almost always over 8 mm.; 2 or 3 thyridia present in each wing (text-fig. 1). Subgenus Agulla ..... 3.

2. Pterostigma at most twice as long as broad ..... *distincta* Banks.
Pterostigma four times as long as broad ..... *minuta* Banks.

3. Pronotum unicolored ..... 4.
Pronotum bicolored ..... 6.

4. Pronotum yellow or light yellowish brown; abdominal sternites yellow ..... *modesta*, n. sp.
Pronotum reddish brown; abdominal sternites dark reddish brown or black ..... 5.

5. Prothorax slightly flattened in the posterior half ..... *bifurca* Banks.
Prothorax normal (rounded) ..... *unicolor*, n. sp.

6. First antennal segment darker than the following ones ..... 7.
First antennal segment not darker than following ones ..... 8.

7. Pterostigma 3–4 times as long as broad, often bicolored ..... *bicolor* Alb.
Pterostigma 6–8 times as long as broad, never bicolored[13] .. *adnixa* Hagen.

[13] A few specimens of *arizonica*, *astuta*, and *bicolor* also fall in this category.

8. Pterostigma about 6 times as long as broad..... *occidentis*, n. sp.
   Pterostigma only 4 or 5 times as long as broad..... 9.
9. Pterostigma about 5 times as long as broad[14]. *arizonica* Banks, *bractea*, n. sp.
   Pterostigma about 4 times as long as broad[15]. *assimilis* Alb., *astuta* Banks.

Subgenus *Agulla*

Agulla adnixa (Hagen)

Plate 2, figs. 8, 9

Raphidia adnixa Hagen, 1861, Syn. Neurop. N. A., p. 195. Hagen, 1867, Trans. Ent. Soc. London, 5, p. 498. Albarda, 1891, Tijdschr. v. Ent., 34, p. 146, pl. 9, fig. 26.

Glavia adnixa Navas, 1918, Mon. Rafid., p. 29.

Raphidia oblita Hagen, 1861, Syn. Neurop. N. A., p. 195. Hagen, 1867, Trans. Ent. Soc. London, 5, p. 498. Albarda, 1891, Tijdschr. v. Ent., 34, p. 149, pl. 9, fig. 25.

Glavia oblita Navas, 1918, Mon. Rafid., p. 31.

♂. Length of fore wing, 8–11 mm.; width, 2.3–3.2 mm.; stigma long, usually light yellow, 6–8 times as long as wide. Head mostly black, posterior half of clypeus black or reddish brown; first antennal segment darker than the following segments. Prothorax bicolored, the posterior half bearing the usual pattern, the anterior half brown or light-brown; meso- and metanotum and abdominal sternites black or very dark brown, the posterior margins yellow (usually); harpogones usually black proximally, yellow-brown distally. Legs light or dark brown. Prothorax about 2½ times as long as thick. Harpogones almost always wide apart, exposing the parameres, which consist of a pair of curved teeth, slightly variable in shape (figs. 8, 9).

♀. Length of fore wing, 8–12 mm.; width, 2.5–4 mm.; color and other characteristics as in male.

Types (♂ ♀).—"California; Oregon (Willcox, Berlin Museum)."

Distribution.—CALIFORNIA (entire state except very arid regions), late March to late June; OREGON (Mt. Hood, Steen Mts., Portland, Blodgett, Hood River, Warner Mts., Corvallis, La Grand, Ashland, Wallawa Mts., Newport, Crater Lake, Klamath Falls, Cannon Beach, Dever, Albany, Forest Grove), April 15 to August 1; WASHINGTON (Forks, Monroe, Longmire, Mt. Adam, Tenino, Wawai, Almata,

[14] *A. bractea* has been found only in southern California; *arizonica* is widely distributed.

[15] *A. astuta* is known only from California; *assimilis* occurs in several neighboring states as well.

Yakima City, Tieton Canyon, Asotin, Waterville, Molson), May 9 to July 28; southern BRITISH COLUMBIA (Seton Lake, Vernon, Victoria, Oliver, Royal Oak, Kelowna, Kaslo, Merrit, Agassiz, Keremeos, Saawich, Yale, Creston, Goldstream, Aspen Grove, Wellington, Duncan), April 28 to July 27; ALBERTA (Waterton, June 1–July 15); IDAHO (Beaver Canyon, July 23; Cedar Mt., Moscow, June 24; Boise, June 13; Moscow Mts., May 26, July 7–8; Craig Mts., June 8; Giveout, July 7; Collins, July 27); MONTANA (Ravalli Co., May 20–23, June 10, July 8; Helena, July; Glacier National Park, July 7); WYOMING (Yellowstone National Park, June 19, July 7, Aug. 1; Jackson, 6600 ft., July 13–17); NEVADA (Carson City, June 26; Verdi); UTAH (Salt Lake City, June 4, 10, 24; American Fork Canyon, July 25; Logan, June 20; Eureka, June 4; Wasatch, July 27; La Sal Mts., 9000 ft., July; Ogden, July 25); COLORADO (Ward, 9500 ft., July 18; Ute Creek, 9000 ft., July 8; Aspen, July 24–27; Ranger Sta., Summit Co., 8211 ft., July 12; Steamboat Springs, May 27; Chimney Gulch, Golden, July 7; Mendo Peak, March 25); NEW MEXICO (Santa Fe Co., July 23; Estancia, Torrance Co.); ARIZONA (Grandview, Johnson Co., June 17; Grand Canyon National Park; Williams, May 30; Catol Springs, April 22; Flagstaff, July 4, H. F. Wickham).

This is the commonest North American species of the snake-flies, and a widely distributed one. Its range is equal to that of the genus in the Nearctic region, except perhaps for southern Arizona, where very little collecting has been done. The male is the most easily recognized of all our species because of the unique form and prominence of the parameres.

Although I have not seen the type of *adnixa* in the Berlin Museum, there is no question of the identity of this species or of the synonymy of *oblita*. Hagen's original account of this species included no description of the genital structure of the male, but in a later paper (1867) he states that the penultimate abdominal segment was very much like that of the European *media* (=*notata*) which he describes as having a "little curved tooth within." There is only one Nearctic species with such a structure. Hagen separated *oblita* from *adnixa* by a few differences in detailed coloration, and a slightly shorter pterostigma, characteristics which are of course worthless in the Raphidiidæ. Unfortunately, the type of *oblita* has been destroyed but in the later paper mentioned above (1867), he includes *oblita* with *adnixa* in his statement regarding the curved tooth, so the identity of the two species is certain. There is a slight amount of variation in the shape of the tooth-like parameres, but even the extremes (shown in figs. 8 and 9) are not sufficient to cause confusion.

Agulla arizonica (Banks)

Plate 2, fig. 14

Raphidia arizonica Banks, 1911, Trans, Amer, Ent. Soc., 37, p. 338, pl. 11, fig. 8.

Glavia arizonica Navas, 1918, Mon Rafid., p. 30.

♂. Length of fore wing, 11–13.5 mm.; width, 3–4 mm.; pterostigma about 5 times as long as broad. Head mostly black or very dark reddish brown; posterior half of clypeus dark reddish brown; first antennal segment usually as light in color (yellow) as the following segment, but often darker, as in the type specimen; pronotum bicolored, the posterior half dark brown or black, the anterior half light brown or brown; rest of thorax and abdomen dark brown or almost black above; abdominal sternites usually dark brown, the posterior margins almost always margined with yellow; harpogones usually uniformly light brown or brown, occasionally black proximally. Prothorax two and one-half to three times as long as thick; parameres, a pair of flat, ribbon-like plates, the extremities curved outward, the lower end almost always projecting beyond the closed harpogones; the upper and lower edges of the parameres bear numerous spines.

♀. Length of fore wing, 10.5–15 mm.; width 3.5–4.5 mm.; color and other characteristics as in the male.

Holotype (♂).—Phoenix, Arizona (undated); Oslar; in the Museum of Comparative Zoology.

Allotype, by present designation.—Mono Lake, California, June 17, 1917, C. L. Fox; in California Academy of Sciences.

Distribution.[16]—California (entire state except very arid areas), March 20 to July 23; Oregon (Mt. Hood, Baker, Klamath Falls, Fremont National Forest, Hood River, Corvallis), May 13 to August 8; Washington (Yakima City, Waterville, Spokane, Blue Mts., Wenatchee, Wawawai, Tacomina, Olympia), May 3 to July 30; British Columbia (Nicola Lake, June 11, 1922, F. R. Buckell; Chilcotin, May 18, June 16, 1920, F. R. Buckell; Keremeos, May 8, 1923, June 18–20, 1923, P. N. Broom, C. B. Garrett; Lyttory, May 21, 1919, W. B. Anderson; Agassiz, May 19, 1927, H. H. Ross; Scranich, May 17, 1919, W. Downes); Alberta (Waterton, June 24, 1923); Montana (Camp Creek, Ravalli Co., July 3, 1933, W. L. Jellison); Idaho (Cedar Mt., Moscow, July 24, 1920, M. C. Lane; Wardner, July 16, 1929, R. A. Flock; Victor, July 11, 1920); Wyoming (Yellowstone National Park, June 26, 1907, W. Robinson); Colorado

[16] These localities are the ones at which males have been taken.

(Sierra Blanca, July 20, 11,500 ft.; Lyons, August 1, 1929; Estes Park, July 11, A. L. Melander; Boulder; Golden, July 7, 1907, Oslar; Roan Mts., June 15, 1921); UTAH (American Fork Canyon, June 21); ARIZONA (Phoenix; Flagstaff, June 4; Williams, May 26, June 15–June 30, A. A. Nichol; St. Catalina Mts., Tucson, alt. 8500 ft., May 12, 1928, A. A. Nichol).

This is the most widely distributed species of Agulla, extending from the extreme southern part of Arizona to well into British Columbia a hundred miles further north than any other species.

Although the males are easily recognized by the nature of the parameres, the females cannot be distinguished with any degree of certainty from those of *assimilis* and some other species. The first antennal segment, which is always yellow in *assimilis*, is also usually yellow in *arizonica*, even though this is not true of the type specimen. The statement made by Lestage, who placed *assimilis* and *arizonica* in different genera, that the branching of Rs is not alike in these species, is not true. The records of the males of *assimilis* and *arizonica* show that the former is not only a much rarer species but that it is confined to a much smaller area, so that most females which have the characteristics of these species can be referred to *arizonica* without a very large percentage of error.

Agulla modesta, n. sp.

Plate 2, fig. 13

♂. Length of fore wing, 10–11 mm.; width, 3.5–4 mm.; pterostigma long, 9 times as long as wide. Head mostly reddish, the black area reduced more than in other species; clypeus with some reddish brown proximally, the rest being yellowish brown; first antennal segment yellow; pronotum uniformly colored, usually more or less straw yellow, sometimes light brown; only a faint suspicion of the dark pattern is visible on the posterior part of the pronotum; rest of thorax and abdomen above light to dark brown; abdominal sternites entirely yellow; harpogones yellow; wing veins light brown. Prothorax 2½ times as long as thick; harpogones broad, without lobes, the epiprocts longer than in other species. Parameres, a pair of flat, ribbon-like plates, with a large *ventral* lobe at the base, and a distinct bend at the distal extremity.

♀. Length of fore wing, 10–12 mm.; width, 3.5–4.2 mm.; color and structure as in male.

Holotype (♂).—Beaver Canyon, Utah; in U. S. National Museum.

No other collecting data are given, but the specimens are part of the Brooklyn Museum Collection.

Allotype.—Same locality as holotype; in U. S. National Museum.

Paratypes.—1♂, 1♀, Beaver Canyon, Utah, in Museum of Comparative Zoology; 1♂, same data, in writer's collection; 2♀, same data, in U. S. National Museum.

This unusual species resembles the following (*banksi*) in general appearance, but the male can at once be distinguished by the shape of the parameres, and the females by the lighter color of the pronotum and the abdomen.

Agulla banksi, n. sp.

Plate 2, figs. 11, 12

♂. Length of fore wing, 8–10 mm.; width, 3–3.5 mm.; pterostigma about 6 times as long as wide. Head mostly black, posterior half of clypeus black or reddish brown; first antennal segment yellow, not darker than the following ones; pronotum uniformly colored, the posterior half not darker than the rest; the whole being a light reddish brown like that of *unicolor,* n. sp.; rest of thorax and abdomen above brown or black; abdominal sternites very dark reddish brown, usually with yellow posterior margins; harpogones mostly yellow or light brown, black or dark-brown proximally (at least in types). Prothorax 2½ times as long as thick; epiproct and harpogones like those of *modesta;* parameres, a pair of broadly oval plates, the upper end tapering almost to a point and overhanging half way down the length of the plate; also a flat, nearly vertical projection is attached to the base of the plate.

♀. Unknown.

Holotype (♂).—Big Bear Lake, California, July 26, 1932; R. H. Beamer; in Museum of Comparative Zoology.

Paratypes.—1♂, Forest Home, San Bernardino Co., California, June 14, 1928, (E. C. Van Dyke); in Museum of Comparative Zoology. 2♂, Forest Home, California, June 11, 1928 (E. C. Van Dyke); 1♂, Forest Home, June 14 (E. C. Van Dyke); all in California Academy of Sciences. 2♂, Big Bear Lake, California, July 26, 1932 (R. H. Beamer); in collection of R. C. Smith. 1♂, same locality data, in writer's collection.

Banksi resembles *unicolor,* n. sp. in general coloration, but has a very different genital structure. The tapering upper part of the parameres, which is constant in the nine types, is a unique feature. The female is probably so similar to that of *unicolor,* n. sp., that it will probably not be recognized until a large series of *banksi* have been collected.

Agulla unicolor, n. sp.

Plate 1, fig. 1

♂. Length of fore wing, 7–8.5 mm.; width, 3–4 mm.; pterostigma 4 to 5 times as long as wide. Head with somewhat more reddish area than in most species; first antennal segment yellow or light brown, never darker than following segments; pronotum uniformly colored, there being a faint trace of the darker pattern on the posterior half; rest of thorax and abdomen above dark brown or black; abdominal sternites brown or black, usually margined with yellow posteriorly; harpogones uniformly yellow, never with black. Prothorax 2½ times as long as thick; harpogones with the inner margins curved inwards and apparently attached to the ædeagus, especially in the anterior half, so that none of the ædeagus and only a small part of the genital chamber is visible unless the harpogones are forced apart; the parameres are nearly always absent, but in a few specimens they are present in the form of a pair of flat, oval plates, either very minute or fairly large (fig. 1).

♀. Length of fore wing, 7–9.5 mm.; width, 3–4.5 mm.; color and structure as in male.

Holotype (♂).—Mariposa Grove, Yosemite National Park, California, July 20, 1932 (F. M. Carpenter); in Museum of Comparative Zoology.

Allotype.—Same collecting data as holotype; in Museum of Comparative Zoology.

Paratypes.—1♂ Eldorado Co., 6300 ft., California, August 22, 1916 (W. M. Giffard); 1♂, 3♀, Carrville, Trinity Co., California, June 18, 1931 (E. C. Van Dyke); 2♀ Carrville, June 22, 1931 (E. C. Van Dyke); 2♂, Sisson, Calif., July 24–25, 1918 (E. P. Van Duzee); 1♂, 2♀, Yosemite, Calif., May 16–17, 1921 (E. C. Van Dyke); 1♂ Crystal Lake, San Mateo Co., Calif., June 18, 1916 (E. P. Van Duzee); 2♀ Crystal Lake, Calif., May 7, 1916 (E. C. Van Dyke); 2♀ Chico, Butte Co., Calif., April 18, 1928 (H. H. Keifer); 1♀ Mt. St. Helena, Calif., May 12, 1926 (E. P. Van Duzee); 1♀, Coffee Creek, Tuolume Co., Calif., June 23, 1931 (E. C. Van Dyke); 2♀, Mark West Springs, Calif., April 27, 1930 (E. C. Van Dyke); 1♂, McCloud, Siskiyou Co., Calif., July 23, 1918 (E. P. Van Duzee); 2♀, Strawberry Valley, Eldorado Co., August 5, August 7, 1912 (E. C. Van Dyke); 1♀, Fallen Leaf Lake, Eldorado Co., Calif., August 1931 (O. H. Swezey); July 14, 1915 (E. C. Van Dyke); 1♀, Truckee, Calif., June 17, 1927 (E. C. Van Dyke); 1♀, Bubbs Creek Canyon, King's River, Alt. 9700 ft.,

Fresno Co., Calif., July 7, 1910 (E. C. Van Dyke); 1♀, Siskyou Co., July 19, 1921 (J. A. Kusche); 1♀, S. Fork, King's River Canyon, 5000 ft., Calif., July 4, 1910 (E. C. Van Dyke); 1♀, Davis Creek, Modoc Co., Calif., July 11, 1912 (C. L. Fox); 1♀, Huntington Lake, Fresno Co., 7000 ft., July 10, 1917 (F. C. Clark); 2♀, Meadow Valley, Plumas Co., 4–5000 ft., June 6, 1928; 1♀, Gold Lake, Sierra Co., Calif., July 10, 1925 (E. H. Nast); 1♀, Gold Lake, July 14, 1921 (C. L. Fox); 1♀, Blue Lake, Lake Co., May 16, 1922 (E. P. Van Duzee); 1♀, Big Pine, Inyo Co., Calif., June 16, 1929 (R. L. Usinger); 1♀, Meadow Valley, Plumas Co., Calif., June 7, 1924 (E. C. Van Dyke); 1♀, Lagunitas, Marin Co., Calif., May 11, 1925 (E. P. Van Duzee); 1♂, 1♀, Homestead Inn, Mt. Hood, Oregon, June 30, 1917 (E. C. Van Dyke); 2♂, 2♀, Homestead Inn. Mt. Hood, July 3, 1927 (E. C. Van Dyke); 1♂, 1♀, Mt. Hood, Oregon, July 25, 1929 (E. C. Van Dyke); 1♂, Eagle Ridge, Klamath L., Oregon, June 2, 1924 (C. L. Fox); 7♂, 2♀, Sparta, Nevada, June 28, 1927 (E. P. Van Duzee); Emigration Canyon, Utah, June 17, 1933 (O. H. Swezey); Mt. Timpanagos, Utah, 8–9000 ft., June 6, 1926 (C. L. Fox); Vivian Park, Utah, July 7, 1922 (E. P. Van Duzee); all in the California Academy of Sciences. 1♂, Yosemite, Calif., May 24, 1921; 1♀, Yosemite Valley, Calif., May 16, 1921 (E. C. Van Dyke); 1♂, Gilroy, Calif., June (Crotch); 1♂, Collins, Idaho, July 27, 1898, 5♂, Reno, Nevada, 2♂, Verdi, Nevada, 1♀, Sparks, Nevada, July 28, 1927 (E. P. Van Duzee); 1♀, Manitou, Colorado (Morrison); all in the Museum of Comparative Zoology. 2♂, Lake Tahoe, Calif., (Hubbard and Schwarz); 1♂, Dunsmuir, Calif., July 20; 2♀, Humboldt Co., Calif., June 13 (Hubbard and Schwarz); 1♀, Mt. Shasta, Calif., July (H. Dyar); 2♂, Kaslo, British Columbia, July 4 (R. P. Currie); 2♂, American Fork Canyon, Utah, June 23–27 (Hubbard and Schwarz); all in the U. S. National Museum. 1♂, Wardner, Idaho, July 16, 1929 (R. A. Flock); in collection at University of Arizona. 1♀, Wallawalla, Washington, June 24, 1921 (A. L. Melander); in Horn collection, Berlin. 1♀, Bozeman, Montana, August 13, 1931 (R. H. Beamer); in collection of R. C. Smith. 1♂, 2♀, Seton Lake, Lillooet, British Columbia, May 28, 1926, 1♂, May 27, 1♂, May 2, 1♂, May 30 (J. M. McDunnough); 1♀, Yale, British Columbia, August 1, 1920 (E. H. Earle); in Canadian Nat. collection, Ottawa. 1♂, 1♀, Mark West Springs, Calif., April 27, 1930 (E. C. Van Dyke); 1♂, Coffee Creek, Tuolume Co., Calif., June 23, 1931 (E. C. Van Dyke); 1♂, Sonora, Calif., May 23, 1931 (E. P. Van Duzee); 1♂, Sisson, Calif., June 25, 1918 (E. P. Van Duzee); 1♀, S. Fork, King's

River Canyon, 5000 ft., July 4, 1910 (E. C. Van Dyke); 1♀, Fairfax, Marin Co., May 7, 1911 (E. C. Van Dyke); 1♀, Huntington Lake, Fresno Co., Calif., July 7, 1911 (F. E. Blaisdell); 1♀, Yosemite, Calif., June 16 (W. M. Giffard); 1♀, Las Altos, Calif., May 7, 1921 (W. M. Giffard); 1♂, Mt. Hood, Oregon, 3–6000 ft., June 21, 1925 (E. C. Van Dyke); 1♂, Wallawalla Mts., Baker Co., Oregon, July 4, 1922 (E. C. Van Dyke); 1♂, Eagle Ridge, Klamath Co., Oregon, May 19, 1924 (C. L. Fox); 1♂, 1♀, Sparks, Nevada, June 28, 1927 (E. P. Van Duzee); 1♀, Sparta, Oregon, July 2, 1922 (E. C. Van Dyke); 1♂, Mt. Hood, Oregon, July 29, 1921 (A. L. Melander); 2♀, Chard, Washington, July 25, 1923 (A. L. Melander); 1♀, Lewiston Hill, Washington, May 31, 1924 (A. L. Melander); 1♀, Seton Lake, British Columbia, May 28, 1926 (J. M. McDunnough); in writer's collection.

Distribution.—California (entire state except very arid areas), April 1 to October 17; Oregon (entire state), April 7 to July 31; Washington (Monroe, Blue Mts., Wallawalla, Chard), June 24 to July 15; British Columbia (Kaslo, N. Bend, Seton Lake, Yale), May 2 to August 8); Idaho (Collins, Wardner, Lewiston Hill, Moscow Mts.), May to July; Utah (Ogden, Vivian Park, Emigration Canyon, Logan Canyon, American Fork Canyon, Mt. Timpanogos), June and July; Nevada (Sparks, Reno, Verdi), June; Colorado (Manitou).

This is a common species which in the past has been confused with several others, especially *adnixa*, *bicolor*, and *arizonica*. It is, however, the most easily recognized of our species, the uniformly reddish brown pronotum being very distinctive from that of all other species, except *banksi*. The males of *unicolor* are unusual for the variation in the parameres; these are absent in fully 95% of the specimens, but are minutely or fully developed in the remaining. It seems very probable that this is a species which is in the process of losing the parameres entirely, a loss which is in my opinion correlated with the firmly closed harpogones. Although this is a common species, it is apparently not so widely distributed as *adnixa* and *arizonica*. It has not yet been turned up in Arizona, New Mexico, Wyoming, and Montana, though I suspect it will eventually be found in the two latter states.

Agulla crotchi (Banks)

Plate 2, fig. 15

Raphidia crotchi Banks, 1924, Bull. Mus. Comp. Zool., 65, p. 429.

♂. Length of fore wing, 7–9 mm.; width, 2.8–3 mm.; pterostigma 6 times as long as wide. Head mostly black or very dark reddish

brown; first antennal segment of type slightly darker than next three segments, but in others species all segments are black; pronotum uniformly colored, either dark reddish brown (type) or black; legs dark brown; rest of thorax and abdomen above and below very dark brown or even black; harpogones are light yellow brown except for the proximal part, where there is the usual black or brown area, and except for a black spot in the distal part or just below the curved tooth. Prothorax 2½ to 3 times as long as high; harpogones of the usual shape, though there is a small, black or dark brown lobe distally just below the curved tooth; parameres are peculiarly modified, each one consisting of two parts; one part is a small triangular, heavily chitinized plate, and the other is a weakly chitinized fleshy membrane with a distinct fold but bearing the short spines characteristic of most of the parameres in Agulla.

♀. Unknown.

Holotype (♂).—"California" (Crotch); in the Museum of Comparative Zoology.

In addition to the type I have seen only three other specimens, all males, of this species; two were taken at Yosemite, California (June 5 and May 17, 1921) and the third at Mt. St. Helena, California (March 15, 1930), all by Dr. Van Dyke. The first specimen is now in the writer's collection, and the others in the California Academy. Although rare, this species is distinctive, the parameres being very different from those of any other species. The whole insect is unusually dark in color, though this is not quite so noticeable in the type as in the new specimens.

Agulla directa, n. sp.

Plate 1, fig. 3

♂. Length of fore wing, 7.5–9 mm.; width, 2–2.5 mm.; pterostigma about 5 times as long as wide. Head mostly black; first antennal segment darker than the following ones; pronotum bicolored; rest of thorax and abdomen above black with some brown, each abdominal segment (in type) with a triangular yellow patch on the posterior margin; abdominal sternites black or nearly so, with or without yellow posterior margins; harpogones mostly black, with some yellow distally. Prothorax 2 to 2½ times as long as broad; parameres, a pair of thick, folded, slightly fleshy structures, roughly oval in outline, with the outer margin thickened, heavily chitinized, and bearing short spines; each paramere is shaped very much like the human ear.

♀. Unknown.

Holotype (♂).—Oroville, California, April 17, 1928 (H. Keifer); in California Academy of Sciences.

Paratypes.—1♂, Oroville, California, March 17, 1928 (H. Keifer); in Museum of Comparative Zoology. 1♂, Mt. Diablo, California, May 29, 1919 (E. C. Van Dyke); in California Academy of Sciences.

This is another uncommon Californian species, with a very restricted range. The parameres are so peculiar that if only one specimen were known with such a structure, it would probably be regarded as a monstrosity; but since three identical specimens have been found (two at the same locality and one 80 miles distant), there can be no question of the validity of this species.

Agulla flexa, n. sp.

Plate 2, fig. 10

♂. Length of fore wing, 9 mm.; width, 3 mm.; pterostigma about 7 times as long as wide. Head with the usual coloration; first antennal segment darker than the following ones; pronotum bicolored; rest of thorax and abdomen above dark brown or black; abdominal sternites black, margin with yellow (in types); harpogones yellow with the proximal part dark brown. Prothorax 3 times as long as thick; harpogones very unusual, there being a lobe extending towards the center of the genital segment just below the curved tooth; this lobe is larger than that in any of our other species; parameres reduced to a pair of thick, chitinous, semi-circular structures, with vestiges of ridges above and below, the whole piece being covered with short spines.

♀. Unknown.

Holotype (♂).—Jemez Mts., New Mexico, June 18 (Woodgate); in Museum of Comparative Zoology.

Paratype.—1♂, Williams, Arizona, June 10 (Barber and Schwarz); in U. S. National Museum.

This curious species will probably be more plentifully represented in collections when more extensive collecting has been done in New Mexico and Arizona. Nothing comparable to the form of the parameres exists in the other species of Agulla, so that the males at least are very readily identified. Mr. Caudell had previously recognized the National Museum specimen as belonging to a new species, but permitted me to do the describing.

Agulla bicolor (Albarda)

Plate 2, fig. 20

Raphidia bicolor Albarda, 1891, Tijds. Ent., 34, p. 152; pl. 8, fig. 24.
Raphidilla bicolor Navas, 1918, Mon. Rafid., p. 51.
Raphidia occulta Banks, 1905, Trans. Ent. Soc. Amer., 32, p. 4.
Glavia occulta Navas, 1916, Mem. R. Acad. Cienc. Art, 12, p. 509; 1918, Mon. Rafid., p. 31, fig. 15.

♂. Length of fore wing, 8–10 mm.; width, 3–3.5 mm.; pterostigma 3–4.5 times as long as broad, either uniformly colored (yellow) or bicolored, the proximal half being brown or dark brown. Head with usual coloration; first antennal segment darker than the following ones; pronotum bicolored, the anterior half being brown, the posterior half very dark brown; rest of thorax and abdomen above very dark brown or even black; abdominal sternites brownish black, usually with yellow posterior margins; harpogones dark brown proximally, yellow distally. Prothorax 2½ to 3 times as long as thick; harpogones of usual form; parameres, a pair of nearly flat plates, strongly chitinized, with a single straight ridge traversing the plate just below the mid-line, and a projecting shelf-like ridge, armed with short teeth, at the very bottom of the plate.

♀. Length of fore wing, 9–11 mm.; width, 3.2–3.8 mm.; otherwise like male.

Cotype (♂ ♀).—"Colorado"; in MacLachlan collection (4♂, 6♀).

Distribution.—California (entire state, except very arid regions), April 1 to July 17; Oregon (Klamath Falls, Wallawalla Mts., Klamath Lake, Lake Co., Mt. Hood, Portland), May 25 to July 28; Washington (Tieton Canyon, June 20, 1932, A. R. Rolfe; Toppenish, May 4, 1926, W. Downs); British Columbia (Oliver, May 7–May 23, 1923, C. B. Garrett; Osoyoos, May 10, 1923, P. N. Vroom); Utah (Cedar City, June 22, 1933, O. H. Swezey; Beaver Canyon; Wasatch Mts., June 20, 1885); Nevada (Steamboat Springs, June 6, 1930; Carson City, June 25, 1929, E. P. Van Duzee; Ormsby Co., July 6, Baker); Colorado (Paonia, June 14, 1926, E. C. Van Dyke); New Mexico (Jemez Mts., July 25; Pecos, June 21); Arizona (Grand Canyon, May 10, 1903, Hubbard and Schwarz; Prescott, May 18, 1902).

The name *bicolor* was given to this species by Albarda because of the bicolored stigma in the specimens which he had. Unfortunately, the coloring of the stigma is decidedly variable and only about one-third of the specimens have a distinctly two-colored one. I have not been

able to see the types of this species, since they are in the MacLachlan collection; but of all of the Nearctic species of Agulla there is only one which ever shows a two colored stigma. There can be no question, therefore, that we have correctly identified Albarda's species. Banks' *occulta* was based upon a specimen of *bicolor* in which the stigma was uniformly colored; an examination of the type of *occulta* shows that the genitalia are exactly like those of the specimens with the bicolored stigma.

The males of this species are best identified by the prominent shelf-like ridge on the bottom of the parameres. Those females possessing the two colored stigma can easily be recognized by that characteristic. When the stigma is not bicolored, it is either a uniform yellow or a uniform brown. The distinctly brown stigma is usually shorter than the yellow one, so that females with a rather short brown stigma (about 3 times as long as wide) are almost certainly *bicolor*. The females possessing the yellow stigma cannot be recognized as belonging here unless they have been collected with a series of males.

Agulla assimilis (Albarda)

Plate 2, figs. 18, 19

Raphidia assimilis Albarda, 1891, Tijdschr. Ent. 34, p. 144; pl. 8, fig. 23.
Agulla assimilis Navas, 1914, Bol. Soc. Arag. Cienc. Nat., 13, p. 66.
Agulla assimilis Navas, 1918, Mon. Rafid., p. 26; fig. 13.
Agulla bagnalli Navas, 1914, Bol. Soc. Arag. Cienc. Nat., 13, p. 66.

♂. Length of fore wing, 10–16 mm.; width, 3.8–5 mm.; pterostigma about 4 times as long as wide. Head with the usual color markings; first antennal segment light yellow, not darker than the following segments; pronotum bicolored, the posterior half marked with the usual pattern; rest of thorax and abdomen above dark brown or black; sternites dark brown or black the posterior margins often yellow; harpogones usually light brown, sometimes bordered with black proximally. Prothorax 2½ to 3 times as long as high; harpogones of the usual shape; parameres, a pair of suboval plates, with 3 (rarely 4) serrate, horizontal or oblique ridges.

♀. Length of fore wing, 10–17 mm.; width, 3.6–5 mm.; color and structure like male.

Holotype (♀).—Vancouver Island, British Columbia; in the MacLachlan collection.

Distribution.—CALIFORNIA (Meadow Valley, Plumas Co.; Fallen Leaf Lake, Eldorado Co.; Lassen National Park; Hamilton Lake,

Truckee, Sequoia National Forest, Big Flat, Trinity Co., Redwood Canyon, Contra Costa Co.; Lake Tahoe, Boulder Oaks), May 23 to August 9; OREGON (Mt. Hood, 3–6000 ft., June 25, 1923, E. C. Van Dyke); BRITISH COLUMBIA (Victoria, June 12, 1916, W. Downs; Departure Bay, April 30, 1909; Lytton, July 12, 1922, R. Glending; Seton Lake, Lillooet, May 23, 1926, F. S. Carr; Kaslo, July 2; Saanich, July 12, 1926, W. Downs); ALBERTA (Waterton, July 16–22, 1931, F. S. Carr).

This is the largest of our species of Agulla, though some specimens are well within the average of other species. I have not seen the type of this species, but the size of the type alone (30 mm. in expanse) indicates that Albarda had either *arizonica* or the species which I have identified as *assimilis*, and the type locality being Vancouver Island, where the present species is particularly common, is strong evidence that Albarda's species has been correctly determined. An examination of the type specimen, which is a female, would not of course provide any further information. A certain amount of uncertainty is associated with the identity of Navas' species *bagnalli*. This was originally described by Navas because he thought the type locality of his specimen, a male, was Victoria, Oceania; but after he discovered later that the locality of his specimen (*bagnalli*) was Victoria, Vancouver Island, he synonymized the latter with *assimilis*, assuming that his specimen was the male of that species. I have not seen Navas' type, which is in the Oxford Museum, but since the specimen was a very large one and the type locality Victoria, Navas' conclusion is probably correct. The only other species to which *bagnalli* might belong is *arizonica*, in which case it would of course become a synonym of that species.

The parameres of *assimilis* are subject to more variation than those of most other species of Agulla. The shape of the plates is quite constant (compare figures 18 and 19), but the arrangement of the ridges is not so uniform. There are usually the three ridges shown in figures 18 and 19, the two larger ones being below the middle line of the plate; but the top ridge may be either at the very edge as in figure 18, or submarginal as in figure 19; in the latter case there is rarely a fourth marginal ridge at the very top.

The distribution of *assimilis* is much more restricted than that of *arizonica*, for it has thus far only been found in California, Oregon, British Columbia, and Alberta. Banks (1903) recorded *assimilis* from Arizona and Colorado, but his specimens undoubtedly belonged to *arizonica*.

Agulla bifurca (Banks)

Plate 2, fig. 17

Raphidia bifurca Banks, 1920, Bull. Mus. Comp. Zool., 64, p. 327.

♂. Length of fore wing, 13 mm.; width, 4 mm.; pterostigma about 5 times as long as wide; costal space unusually narrow. Head with the usual coloration, but the reddish areas extending more anteriorly than usual; first antennal segment yellow, not darker than the following ones. Pronotum uniformly colored, in that the anterior half is not distinctly lighter than the posterior, although the usual brown pattern is visible on the posterior half; rest of thorax and abdomen above dark brown or black; abdominal sternites dark reddish brown or black, sometimes margined with yellow (in all known specimens). Prothorax 2½ times as long as high; posterior half flattened or at least distinctly not as rounded as in other species of Agulla. Harpogones of the usual shape; parameres, a pair of flattened, elongate-oval, plates, bearing three shelf-like ridges, almost parallel.

♀. Length of fore wing, 13 mm.; width, 4 mm.; color and structure as in the male, including the flattened prothorax.

Cotypes (♂ ♀).—♂, Wellington, British Columbia, May 9, 1898; ♀, May 3, 1897; both in the Museum of Comparative Zoology.

In addition to the types I have seen only one specimen of this species—a male in the California Academy Collection from Fallen Leaf Lake, Tahoe, Calif., June 25, 1915 (E. C. Van Dyke). The finding of a specimen in California suggests that the insect probably occurs in Oregon and Washington. *Bifurca* can easily be recognized by the combination of the unicolored and flattened pronotum and the narrowed costal space of the fore wings; the male of course is best identified by the parameres, which are longer than those of *assimilis*, and have the top ridge well down towards the middle.

Agulla occidentis, n. sp.

Plate 2, fig. 21

♂. Length of fore wing, 12–15 mm.; width, 3.5–4 mm.; pterostigma 6 times as long as wide. Head with the usual coloration; first antennal segment light brown, not darker than the following ones; pronotum bicolored, the anterior half being light brown or brown; rest of thorax and abdomen above dark brown or black; abdominal sternites dark brown or black, not usually margined with yellow; harpogones yellow, with brown or dark brown proximally. Prothorax almost 2½ times as long as wide; harpogones of the usual form;

parameres, a pair of *convex* elongate plates, usually dark reddish brown, with 3 or 4 shelf-like ridges; the plates are not flat, as in *assimilis*, but decidedly cylindrical; the top ridge is frequently very small and the position of the ridges is somewhat variable.

♀. Length of fore wing, 11–15.5 mm.; width, 4–4.2 mm.; color and structure as in the male.

Holotype ♂.—Pine Crest, California, July (Johnson); in California Academy of Sciences.

Allotype ♀.—Same collecting data as holotype; in California Academy of Sciences.

Paratypes.—1♂, Mt. Hood, Oregon, July 2, 1927 (E. C. Van Dyke); 1♂, Mt. Hood, Oregon, July 25, 1924 (E. C. Van Dyke); 1♂, Weed, Calif., June 27, 1922; all in California Academy of Sciences. 1♂, Fallen Leaf Lake, Tahoe, Calif., July 1, 1919 (E. C. Van Dyke); 1♀, Pine Crest, Calif., July; both in Museum of Comparative Zoology 1♂, Pine Crest, Calif., July; 1♂, 8 mi. West of Ft. Klamath, Oregon, August 3, 1930 (H. A. Scullen); 1♂, Strawberry Valley, Eldorado Co., August 7, 1912 (E. C. Van Dyke); all in the writer's collection.

Occidentis is closely related to *assimilis* and I have been unable to find any structural differences between the females of these two species; the two female types of *occidentis* have been identified as that species because of their association with the males. The male of *occidentis* is readily recognizable by the convexity of the parameres, this being the only species possessing that characteristic.

Agulla bractea, n. sp.

Plate 2, fig. 16

♂. Length of fore wing, 13 mm.; width, 4 mm.; pterostigma 5 times as long as wide, very light yellow; costal space unusually broad. Head with the usual coloration; first antennal segment yellow, not darker than following ones; pronotum bicolored, the anterior half brown; rest of thorax and abdomen above dark brown or black; abdominal sternites brown or dark brown; harpogones yellow or light brown, with a darkened proximal part. Prothorax 2½ times as long as thick; parameres, a pair of very broad, flat plates, containing two very large shelf-like ridges.

♀. Length of fore wing, 15 mm.; width, 5 mm.; color and structure as in male.

Holotype ♂.—San Gabriel Mts., 3500 ft., Calif., June 11, 1910 (F. Grinell, Jr.); in Museum of Comparative Zoology.

Allotype.—Laguna, San Diego Co., Calif., June 4, 1926 (W. S. Wright); in San Diego Museum, California.

Paratypes.—1♂, Forest Home, San Bernardino Co., Calif., June 11, 1928 (E. C. Van Dyke); 1♂, Forest Home, Calif., June 13, 1928 (E. C. Van Dyke); both in California Academy. 1♂, Laguna, San Diego Co., Calif., June 4, 1926 (W. S. Wright); in San Diego Museum. 1♂, Forest Home, San Bernardino Co., June 14, 1928 (E. C. Van Dyke); in writer's collection.

This is another large species which simulates *assimilis* and the female of which seems to be indistinguishable from that of the latter species. The male is easily recognized by the exceedingly broad parameres, and the acute upper and lower margins of the plates.

Agulla astuta (Banks)

Plate 2, fig. 22

Raphidia astuta Banks, 1911, Trans. Amer. Ent. Soc., 37, p. 338–339.
Glavia astuta Navas, 1918, Mon. Rafid., p. 30.

♂. Length of fore wing, 9–12 mm.; width, 3–4 mm.; pterostigma about 4 times as long as broad. Head mostly black; first antennal segment either darker or lighter than the following ones (lighter in types); pronotum bicolored, the posterior half dark brown with the usual pattern in black, the anterior half light brown or brown; rest of thorax and abdomen above dark brown or black; abdominal sternites dark brown or black, occasionally with yellow posterior margins; harpogones dark brown proximally, light brown or yellow distally. Prothorax 3 times as long as thick. Harpogones as usual; parameres, a pair of flattened plates, *obliquely placed*, the bottom being nearer the ædeagus than the apex; two ridges present, one near the bottom, the other just above the middle.

Cotypes.—1♂, Pasadena, California, May 31, 1919 (F. Grinnell, Jr.); 1♂, San Gabriel Mts., Pasadena, California, June 17 (F. Grinnell, Jr.). 1♂, Mt. Wilson, Pasadena, California, June 5, 1904 (F. Grinnell, Jr.); in Museum of Comparative Zoology.

Distribution.—California (Carmel, Monterey Co., March 25, 1919, E. P. Van Duzee; Palmdale, April 20, 1932, E. P. Van Duzee; Lompoe, 13 mi. east, April 21, 1932, E. P. Van Duzee; Redwood Canyon, Contra Costa Co., May 28, 1905, E. C. Van Dyke; Mt. Tamolpais, Marin Co., May 7, 1911, E. C. Van Dyke; Pasadena, May 3 to June 30; San Diego Co., May 26, 1927).

This species resembles *adnixa* superficially. The female can be recognized by the light colored first antennal segment, though unfor-

tunately this is not an absolutely constant characteristic. The parameres of the male are unique in being obliquely situated, a peculiarity which is not shared by any other species of Agulla in which the parameres are in the form of flat plates. So far there are no records of this insect outside of California.

Agulla singularis, n. sp.

Plate 2, fig. 23

♂. Length of fore wing, 12 mm.; width, 4 mm.; pterostigma 5 times as long as wide. Head with the usual coloration; first antennal segment light brown, not darker than the following ones; pronotum bicolored, the anterior half brown, the posterior half almost black; rest of thorax above grayish brown; abdomen above dark brown with some lighter brown; abdominal sternites yellow and harpogones yellow. Prothorax 2¼ times as long as thick; harpogones as in *assimilis;* parameres, a pair of very large oval plates, much larger proportionally than those of any other species; 3 ridges are present, one at the middle, and one at both the bottom and top (in type).

♀. Unknown.

Holotype (♂).—Banning, California, May 29, 1928 (E. C. Van Dyke); in California Academy of Sciences.

Although there is only one specimen of this species in the material which has passed through my hands, I am nevertheless convinced that the species is a valid one, because of the remarkably large size of the parameres. The positions of the upper and lower ridges of the parameres will probably turn out to be slightly variable when additional specimens are found.

Agulla neglecta, n. sp.

Plate 1, fig. 2

♂. Length of fore wing, 15 mm.; width, 4 mm.; pterostigma a little less than 5 times as long as wide. Head with the usual coloration; first antennal segment light brown, not darker than the following ones; pronotum bicolored, the anterior half brown; rest of thorax above light brown; abdomen above dark brown or black; abdominal sternites yellow and harpogones entirely yellow. Prothorax 2½ times as long as thick; harpogones very long and narrow (fig. 2); parameres, a pair of very small oval plates, with one shelf-like ridge at the bottom, as very short, weak ridge at the middle, and another small one at the top.

♀. Unknown.

Holotype (♂).—East Lake, California, June, 1883 (Turner); in U. S. National Museum.

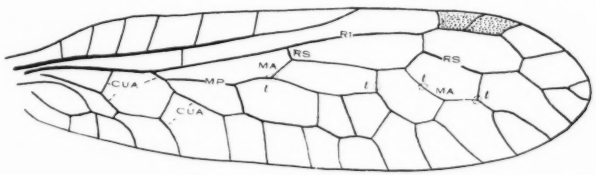
This large species is made distinctive not only by the long harpogones, but also by the very small size of the parameres, the minuteness of which is exaggerated by the length of the harpogones.

Subgenus *Alena*[17]

Agulla (*Alena*) *minuta* (Banks)

Plate 1, fig. 6

Raphidia minuta Banks, 1903, Proc. Ent. Soc. Wash., 5, p. 239; pl. 4, fig. 7. Banks, 1911,[18] Trans. Amer. Ent. Soc., 37, pl. 11, figs. 2.
Alena minuta Navas, 1916, Mem. Acad. Cienc. Barc. 12, p. 510. Navas, 1918, Mon. Rafid., p. 35.



TEXT-FIGURE 6. Fore wing of *Agulla* (*Alena*) *minuta* (Banks); lettering as in text-figure 1.

♂. Length of fore wing, 7 mm.; width, 2 mm.; pterostigma 3½ to 4 times as long as wide. Head coloration as in other species, but subject to even more variation; first antennal segment dark brown, darker than the following ones; prothorax bicolored, the anterior half almost light brown, posterior half with the usual pattern in very dark brown; rest of thorax and abdomen above reddish brown or almost black; abdominal sternites reddish brown to black; harpogones light reddish brown. Prothorax three times as long as thick; harpogones very large, terminating in two pairs of cylindrical processes; one of these arise from the dorsal terminal part of the harpogones,

[17] *Agulla australis* (Banks), from Lower California, probably belongs to Alena.

[18] The figure of the pterostigma of *minuta* in Banks' 1911 paper (Trans. Amer. Ent. Soc., pl. 11, fig. 10) is not correct; this figure in reality depicts the pterostigma of *distincta* Banks.

and is smoothly curved and elongate, extending well beyond the rest of the genitalia; the other pair arise from the ventral edge of the harpogones and extend directly upwards, terminating in a pair of small hooks; the epiproct terminates in a pair of slightly curved, cylindrical processes, pointing downward; parameres, a pair of very long, curved hooks, which are directed towards the roof of the genital chamber (fig. 6).

♀. Length of fore wing, 7–8 mm.; width, 2–2.5 mm.; pterostigma 4 times as long as wide; color and structure as in male.

Holotype (♂).—Williams, Arizona, June 1[19] (Barber and Schwarz); in U. S. National Museum.

Paratypes.—1♂, Williams, Arizona, July 5 (Barber and Schwarz); in Museum of Comparative Zoology. 1♀, Flagstaff, Arizona, July 6; 1♀, Las Vegas, New Mexico, August 6; 1♂ Williams, Arizona, August 1; 2♀, Williams, Ariz., July 17; 2♂, Flagstaff, Ariz., July 3; 1♂, Williams, Ariz., July 27; Williams, Ariz., July 9.

In addition to the types, I have seen the following specimens of this curious little species; 1♂, Mormon Lake, 7000 ft., Arizona, June 12, 1925 (A. A. Nichol); 1♂, Glen Oaks, Arizona, July 19, 1929 (E. D. Ball); 1♂, 2♀, Ft. Wingate, New Mexico, June 1, June 25; 1♂, Beulah, New Mexico, August 13, 1900 (T. D. A. Cockerell); 1♂, 1♀, Mesilla, New Mexico. It is probable, judging from the collection which has passed through my hands, that *minuta* is restricted to certain parts of Arizona and New Mexico. At any rate, among the thousand or more specimens of snake-flies which I have examined from California, not a single specimen of this insect has turned up.

Both sexes of *minuta* can easily be distinguished from those of the following species of Alena by the shape of the pterostigma; the male genitalia are so very different that specimens of this sex can be separated even without the aid of a lens.

Agulla (*Alena*) *distincta* Banks

Plate 1, fig. 7

Raphidia distincta Banks, 1911, Trans. Amer. Ent. Soc., 37, p. 338; pl. 11, fig. 1, 6.

Alena distincta Navas, 1916, Mem. R. Acad. Cienc. Acad. Barc., 12, p. 510. Navas, 1918, Mon. Rafid., p. 35.

♂. Length of fore wing, 6–7 mm.; width, 1.8–2 mm.; pterostigma,

[19] The date of this specimen was accidentally published in the original description as June 10.

1½ to 2 times as long as wide. Head with the usual coloration; first antennal segment darker than the following ones; pronotum bicolored, but the darker area (black) on the posterior part extends far more towards the front end than usual; the anterior fourth or third of the pronotum is light reddish brown, and the posterior three-fourths or two-thirds is black, their being no trace of the usual pattern; rest of thorax and abdomen above, black or dark brown; abdominal sternites dark brown; harpogones black. Head *usually* wider across the eyes than in *minuta;* prothorax 3 times as long as thick; harpogones wide, but not as long as in *minuta,* and bearing only a single, slender but short process, which is not nearly as long as the epiproct; the epiproct is a single flat, elongate, plate, abruptly curved distally, and bearing at its end two small teeth and a pair of jet black, flat plates; the parameres consist of a pair of long slender hooks, much like those of *minuta* except that they are a little shorter.

♀. Length of fore wing, 7–8 mm.; width, 2 mm.; otherwise like male.

Holotype (♂).—Mt. Pinos, Kern Co., California, June 6, 1904 (F. Grinnell, Jr.); in Museum of Comparative Zoology.

Paratypes.—1 ♀, San Gabriel Mts., Los Angeles Co., California, June 5 (F. Grinnell, Jr.); 1 ♀, San Gabriel Mts., Los Angeles Co., California, 3000 ft., June 17, 1909 (F. Grinnell, Jr.); 1 ♀, Saw Mill Canyon, Kern Co., California, June 6, 1905 (F. Grinnell, Jr.); 1 ♀, Mt. Pinos, Kern Co., California, June 12, 1904 (F. Grinnell, Jr.); all in the Museum of Comparative Zoology.

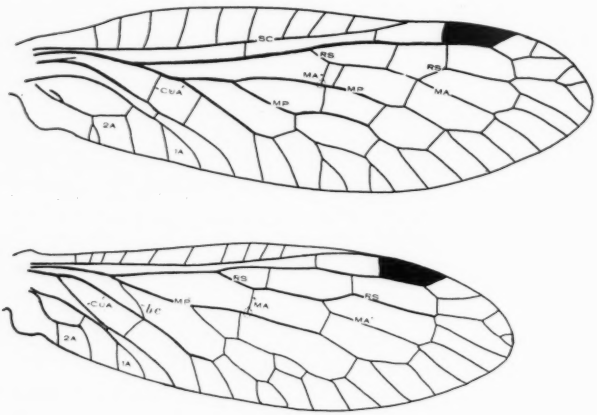
In addition to the types I have seen specimens of this species from the following localities, all in California: 3 ♀, Lebec, alt. 4000 ft., May 13–15, 1928 (J. O. Martin); 1 ♀, Lytle Creek, San Bernardino Co., June 8, 1928 (E. C. Van Dyke); 1 ♀, Independence, Inyo Co., June 14, 1929 (R. L. Usinger).

Distincta resembles *minuta* in general aspect, but differs in having a darker pronotum, a much shorter pterostigma, and surprisingly dissimilar genital structure, except for the parameres. As far as I am aware this insect has not been taken outside California, so that the ranges of the two species of Alena do not overlap.

Family Inocelliidæ

Head longer than wide, always as broad or broader posteriorly than anteriorly; antennæ inserted close together with from 65 to 70 segments, the first segment much larger than the second; clypeus large, very wide; maxillary palpi 4-segmented; labial palpi 3-segmented; mandibles small, with three or four teeth; eyes prominent, but smaller

than in the Raphidiidæ, and placed well back from the clypeal margin; ocelli absent. Prothorax not as long as the head; pronotum expanded laterally, *but not ventrally*, forming a curved hood which covers only the upper two-thirds of the prothorax; meso- and metathoracic segments short, not so long as wide; prothoracic legs attached to the posterior part of that segment; 3d tarsal segment enlarged and flattened, the 4th very small. Male abdomen terminating in a hood-shaped epiproct; harpogones consisting of a pair of convex plates,



TEXT-FIGURE 7. Fore and hind wings of *Inocellia inflata;* lettering as in text-figure 1.

concealing the genital cavity; female abdomen terminating in an epiproct like that of the male; ovipositor about as long as the entire abdomen and sickle-shaped. Fore-wing: costal margin arched, the costal space broadened but not nearly so much as in the Raphidiidæ; Sc terminating beyond the middle line of the wing; Rl without branches, pterostigma not margined or traversed by veinlets; rest of venation like that of the Raphidiidæ. The hind wing is a little shorter and more slender than the fore wing, and the costal space is hardly broadened. In most other respects the venation is like that of the fore wing; Rs arises at about the same level as in the fore wing; MA originates either as in the fore wing or arises from the base of M; the basal cross-vein between M and CuA (see text-fig. 7, bc.) is

always oblique to the latter, never perpendicular as in the Raphidiidæ; CuA divides close to the base of the wing, the anterior branch free from M and MP, the posterior branch not coalescing with 1A; 1A is unbranched, 2A forked. Only one thyridium is present on each wing and that is frequently missing.

Nothing has been published, so far as I am aware, on the internal anatomy of the Inocelliidæ, and very little is known of their biology. Stein was apparently the first to publish (1838) on the life-history of the species of Inocellia, and Schneider later (1843) contributed materially to this subject and the general external anatomy; but since then nothing further has been added to our knowledge of the biology or morphology of these insects. To a large extent this lack of observation during the past ninety years is probably due to the restricted geographical distribution of the Inocelliidæ. According to Schneider the habits and development of these larvæ are like those of the Raphidiidæ. He found the larvæ to occur under the bark of several species of Pinus, and states that the larval period lasts for twenty or twenty-two months, pupation occurring in May. The pupæ develop like that of the Raphidiidæ, becoming more and more active as the time approaches for the adult to emerge. The pupal period (in *I. crassicornis* Schneider) is much shorter than the larval stage, lasting only a few weeks. The general structure of the Inocelliid larvæ is of course similar to that of the Raphidiid larvæ, but certain details are different. The most striking difference is in the number of eyes, there being seven on each side of the head in the Raphidiid, but only four in the Inocelliid larva, two of which are very minute. This smaller number of eyes in the Inocelliid larvæ is especially interesting in view of the absence of ocelli in the adults. The pupal stage of the Inocelliidæ is similar to that of the Raphidiidæ, and as was the case in the latter family the mandibles of the pupæ are almost like those of the larvæ, not like those of the adults.

The family Inocelliidæ, as treated in this paper, consists of two genera only,—Inocellia and Fibla. The latter genus is exclusively European, but the former includes two Nearctic and several Palaearctic species. The difference between these two genera lies, of course, in the position of the point of origin of MA in the hind wing; in Inocellia MA arises from the stem of M almost at the base of the wing, whereas in Fibla it originates at mid-wing. The synonymy of the Inocelliid genera has already been discussed in the preceding pages.

Genus *Inocellia* Schneider

Inocellia Schneider, 1843, Mon. Raphidiæ, p. 84. Albarda, 1891, Tijdschr. Entom., 34, p. 155. Navas, 1918, Mon. Rafid., p. 75.
Negha, Navas, 1916, Mem. Real. Acad. Cienc. Art., 12, p. 510.
Estoca, Navas, 1919, Arxivs Inst. Ciencies, 1919, p. 91.

Genotype—*Inocellia crassicornis* Schneider

Three Nearctic species of this genus have been described (*inflata* Hagen, *longicornis* Albarda, and *hageni* Albarda), but only two of these are valid. In the past these species have been separated by such characteristics as have been used in Agulla (color of body, venation, etc.), and there is no need to include here a detailed discussion of these features; it is sufficient to point out that these characteristics are as unsatisfactory here as in the previous family. The coloration of the head and prothorax differs greatly from that in Agulla: the head is almost solid black, lacking the reddish pattern characteristic of Agulla, and the pronotum is entirely black, except for the margins, which are yellow; but so far as our two species are concerned the coloration is of no specific value. The genital structure is not nearly so complicated as that of the Raphidiidæ and does not provide us with as many taxonomic characteristics as in the latter family. The epiproct is similarly shaped in all the species of Inocellia, but the harpogones show some difference in form; they consist of a pair of curved plates, which taper distally, the very end being recurved inward, and terminating in a small straight tooth. There are no parameres present. In the female, the shape of the 8th sternite is the most dependable means of distinguishing our species. The females are noticeably larger than the males on the average, and attain a size exceeding that of any of the species of Agulla.

The two Nearctic species of Inocellia can be distinguished as follows:

Harpogones elongate, tapering (Plate 1, Fig. 5); posterior margin of 8th sternite of female smoothly rounded (text-fig. 8). . . . . *inflata* Hagen.
Harpogones almost semi-circular (Plate 1, Fig. 4); posterior margin of 8th sternite of female irregularly curved (text-fig. 8). . *longicornis* Albarda.

Inocellia inflata Hagen

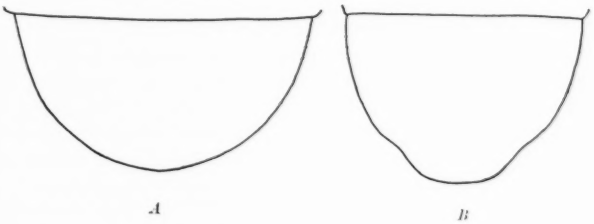
Plate 1, fig. 5

Raphidia inflata Hagen, 1861, Syn. Neur. N. A., p. 196.
Inocellia inflata Albarda, 1891, Tijdsch. Entom., 34, p. 167, pl. 11, fig. 31.

Inocellia hageni Albarda, 1891, Tijdsch. Entom., 34, p. 171; pl. 11, fig. 33. Navas, 1918, Mon. Rafid., p. 80.

Negha inflata Navas, 1916, Mem. R. Acad. Cienc. Art., 12, p. 510.

♂. Length of fore wing, 11–13 mm.; width, 3.2–3.8 mm.; stigma 4 times as long as wide. Head all black except the very posterior part adjacent to the neck which is reddish brown; first and second antennal segments reddish brown, the rest dark grey-brown; pronotum uniformly black, except for the anterior and posterior margins, which are almost yellow; rest of thorax and abdomen above dark brown or black; abdominal sternites reddish brown, with yellow posterior margins; harpogones reddish brown. Head with the characteristic shape of the genus, usually broader posteriorly than anteriorly; length



TEXT-FIGURE 8. Hypandria of *Inocellia inflata* Hagen (A), and *I. longicornis* Alb. (B).

of antennæ variable, in some specimens only as long as the abdomen, in others 1½ times as long as the abdomen; prothorax twice as long as thick; harpogones more slender and longer than those of *longicornis*.

♀. Length of fore wing, 12–17 mm.; width, 3.5–6 mm.; color and structure similar to those of male except that the pterostigma is almost always shorter (about 3 times as long as wide) than in the male; the posterior margin of the 8th sternite is smoothly rounded (text-figure 8).

Neotype (♂), by present designation.—Mariposa Grove, Yosemite, California, July 12, 1927 (F. M. Carpenter); in Museum of Comparative Zoology.

Allotype, by present designation.—Same collecting data as neotype; in Museum of Comparative Zoology.

Distribution.—CALIFORNIA (Lake Tahoe; Lassen National Park; Nevada City; Giant Trees, Tulare Co.; Sequoia National Park, 3–5000 ft.; Gold Lake, Sierra Co.; Meadow Valley, Plumas Co.;

Yosemite; Cypress Ridge, Marin Co.; Cisco; Argus Mts., Saticoy; Los Angeles; San José), April 2 to July 11; OREGON (Homestead Inn, Mt. Hood, July 2, 1927, E. C. Van Dyke; Klamath Falls, June 16, 1922, E. C. Van Dyke; Scio, May 20, 1931); BRITISH COLUMBIA (Keremeos, July 14, 1923, C. B. Garrett); NEVADA (Reno, 1878, Morrison). Albarda records this species from Arizona, but I have seen no specimens from there. The original type locality was given by Hagen as "California."

Hagen's type specimen was unfortunately destroyed in transit to Albarda and I have therefore designated a neotype. Although Hagen's description is far from satisfactory, Albarda's account, which is accompanied by excellent figures, enables easy recognition of this insect. Since Albarda was in constant communication with Hagen and had seen various specimens of *inflata* in European collections named by Hagen, it is almost certain that Albarda had correctly identified the species, even though the type was destroyed before it reached his hands. In describing *hageni*, Albarda was mislead by the usual difference in size of the pterostigma in the females of Inocellia (at least the Nearctic species). In the females of both *inflata* and *longicornis* the pterostigma, although variable in length, is on the average decidedly shorter than in the male. Albarda based *hageni* on a female which in his opinion differed from *inflata* by the color of the head, the shape of a certain cell of the fore wing, and the short pterostigma. The two former characteristics are of course individual in nature, and the latter one is a secondary sexual character of the females of Inocellia. There is a possibility of course that *hageni* is a synonym of *longicornis* rather than *inflata*, a question which can be decided when the type of *hageni* (now in the MacLachlan Collection) becomes available for study.

Inocellia longicornis Albarda

Plate 1, fig. 4

Inocellia longicornis Albarda, 1891, Tijdschr. Entom., 34, p. 169, pl. 11, fig. 32.

Negha longicornis Navas, 1918, Mon. Rafid., p. 75.

♂. Length of fore wing, 11–12 mm.; width, 3.2–3.8 mm.; stigma about 5 times as long as wide. Head nearly all black, with only the posterior border reddish brown; first and second antennal segments reddish brown, sometimes dark brown, the rest of the antennæ being dark brown or grey-brown; pronotum uniformly black, except for the anterior and posterior edges, which are bordered with yellow; rest of

thorax and the abdomen above dark brown or black; abdominal sternites reddish brown, with or without the yellow margins; harpogones reddish brown. Head shaped as in *inflata;* antennæ variable in length, either somewhat shorter than or as long as the fore wing; prothorax twice as long as thick; harpogones broad and short, almost semi-circular in lateral aspect.

♀. Length of fore wing, 12–16 mm.; width, 3.5–5.5 mm.; color and structure similar to those of male, except for the shorter pterostigma; posterior margin of 8th abdominal sternite not smoothly curved (text-figure 8).

Holotype (♂).—"California"; in the MacLachlan Collection.

Allotype, by present designation.—Palo Alto, California; in Museum of Comparative Zoology.

Distribution.—CALIFORNIA (Calaveras; Fairfax, Marin Co.; Mt. St. Helena; Yosemite; Stone Canyon, Monterey Co.; Palo Alto; Sierra Nevada Mts.), April 5 to June 7; OREGON (Homestead Inn, Mt. Hood, July 2–3, 1927, E. C. Van Dyke; Mt. Hood, July 25, 1925, E. C. Van Dyke; Klamath Falls, May 13, 1924; Oakridge, May 30, W. S. Chamberlin); WASHINGTON (Longmire, July 18, 1919, C. L. Fox; Lake Keechius, June 29, 1922, A. L. Melander; Mt. Adams, July 24, 1921, A. L. Melander); BRITISH COLUMBIA (Kaslo, June 24, R. P. Currie; Anderson Lake, D'Arcy, June 17, 1926, J. M. McDunnough); NEVADA (Reno, 1878, Morrison).

As he indicated by the name, Albarda established this species with the belief that the length of the antennæ was a good specific character. This is not the case, however, and the name *longicornis* is an unfortunate misnomer. The antennæ of the Inocelliids contain a large number of segments, usually about 70, so that a very slight difference in the size of the individual segments makes a noticeable result in the length of the entire antenna. At any rate, a study of a series of specimens shows a perfectly gradating series of antennæ in the two Nearctic species of Inocellia, varying in length from hardly half as long as the fore wing to fully as long as the wing, which was the case in Albarda's type specimen.

The males of *longicornis* are easily distinguished from those of *inflata* by the more rounded harpogones; this characteristic was well figured by Albarda, so that although I have not seen his type of *longicornis*, the identity of the species is clear. The female of this insect was not known to Albarda; it differs from that of *inflata* chiefly by the shape of the 8th sternite.

Extinct Raphidiodea

A surprisingly large number of fossil snake-flies have been found in the Nearctic region. Up to the present time eleven species of these insects have been described from the Tertiary of North America, which is equal to the number of extant species previously known from the same area; and in this paper another species, from the Miocene of Colorado, is added to the list. Only one snake-fly has been described from the European Tertiary, but since that is in amber and splendidly preserved, it makes an important contribution to our knowledge of the geological history of these insects. The oldest known members of the order are the Mesoraphidiidæ, which Martynov has described from the Jurassic of Turkestan. One insect wing from the Lower Permian of Kansas (*Permoraphidia americana* Till.) appears to show some affinities with the snake-flies, and has been placed by Tillyard in the Raphidiodea; but its relationship with the Tertiary fossils is so remote that it hardly falls within the scope of this paper.[20]

In classifying the Tertiary snake-flies we are of course handicapped by the lack of well preserved body structures, the fossils consisting chiefly of wings. It is therefore necessary that the family and generic position of these fossils be determined primarily from the wings. Both fore and hind wings of the snake-flies do, of course, possess structures satisfactory for the determination of the family. The fore wings of the Inocelliidæ can be distinguished from those of the Raphidiidæ by the dark and unmargined pterostigma, the more distal origin of Rs, and the absence of the twigging of the veins, the hind wings are at once recognizable not only from these features but also by the oblique cross-vein leading from M to CuA, this cross-vein being perpendicular (or nearly so) to the connected veins in the Raphidiidæ. But the generic position of the fossils belonging to either of these families is not so easily determined from incomplete specimens. The question of the generic position of the fossils has been rendered even more uncertain by the confusion attending Navas' erection of genera based upon unstable characteristics. This circumstance led Cockerell and Custer (1925) to conclude that until the genera of extant species were placed upon a more satisfactory basis, the fossil genera must be regarded as provisional. It was with the hope that the classification advocated in the preceding pages would attain the desired results that I have undertaken to revise the fossil forms.

[20] A discussion of Permoraphidia will be included in the next part (No. 8) of my series of papers on the Lower Permian insects of Kansas.

Through the courtesy of the authorities of several institutions, it has been possible for me to examine the types of all described species of Nearctic Raphidiodea, except two which have unfortunately been lost. The types of four of Scudder's five species are in the Museum of Comparative Zoology; the type of the fifth species (*veterana*) was a part of the Princeton University collection and appears to be lost. Dr. E. M. Kindle, Director of the Canadian Geological Survey, kindly loaned me the type of Handlirsch's *Archiinocellia oligoneura* from the Oligocene of British Columbia; and Professor T. D. A. Cockerell and Dr. H. Rodeck, the types of *mortua* Rohw., *exusta* Cock. and Custer, and *exhumata* Cock., as well as a second fine specimen of *exhumata*. The type of *pulveris* Cock. was originally in the collection of the late Professor H. F. Wickham, but in response to my inquiries regarding this fossil, Professor Wickham kindly donated it to the Museum of Comparative Zoology. The type of *Megaraphidia elegans* Cock., has apparently been either lost or destroyed. I am indebted to Professor Cockerell for the use of some original notes on the types of his species, and especially for his interest and encouragement, which has always been inspiring.

TABLE I.

CHRONOLOGICAL LIST OF TERTIARY RAPHIDIODEA OF NORTH AMERICA

Species	*Horizon*	*Locality*
Raphidia (?) *tranquilla* Scudder, 1891	Miocene	Florissant
Inocellia veterana Scudder, 1891	Miocene	Florissant
Inocellia somnolenta Scudder, 1891	Miocene	Florissant
Inocellia tumulata Scudder, 1891	Miocene	Florissant
Inocellia eventa Scudder, 1891	Miocene	Florissant
Megaraphidia elegans Cockerell, 1907	Miocene	Florissant
Raphidia exhumata Cockerell, 1909	Miocene	Florissant
Raphidia mortua Rohwer, 1909	Miocene	Florissant
Archiinocellia oligoneura Handlirsch, 1910	Oligocene	British Columbia
Raphidia pulveris Cockerell, 1914	Miocene	Florissant
Inocellia exusta Cockerell & Custer, 1925	Miocene	Florissant
Raphidia creedei, n. sp.	Miocene	Creede, Col.

All but one of the eleven described fossil Nearctic snake-flies can be assigned without question to either the Raphidiidæ or Inocelliidæ. The single exception is *Archiinocellia oligoneura* Handl., from the Oligocene of British Columbia. Handlirsch placed this fossil in the Inocelliidæ, as the generic name implies; but there is absolutely no

evidence for this conclusion contained in the very poorly preserved specimen. As shown in Handlirsch's figure (1910, p. 101) only portions of the two wings are preserved and one wing rests upon the other in such a way as to produce a confusion of veins. Even admitting that Handlirsch's restoration of the wings (p. 102) is correct, I fail to find any indication there that the specimen is an Inocelliid. If Handlirsch's figure is correct in so far as the presence of the veins bordering the pterostigma is concerned, then the fossil is surely a Raphidiid. But I am convinced from my examination of the fossil that it is impossible to determine satisfactorily whether or not there are cross-veins bordering the pterostigma. The most that can be said about *A. oligoneura*, in my opinion, is that it is a member of Raphidiodea with uncertain affinities.

With the exception of one species, *Inocellia exusta* Cockerell and Custer (1925), the remaining fossils belong to the family Raphidiidæ, although several have been placed by Scudder and others in the Raphidiidæ. Scudder, who described his species before Albarda's revision (1891) appeared, was misled by an incorrect idea of the difference between Inocellia and Raphidia. In his table of these genera, Raphidia was separated from Inocellia by having the pterostigma crossed by veinlets and by having the wings only three times as long as broad, instead of having an undivided pterostigma and the wings more than three times as long as wide. Neither of these characteristics holds true, however; a great many specimens of Raphidia possess an undivided pterostigma in either all wings or only one, and the relative length of the wings varies greatly in the individuals of a single species far beyond the proportions set by him. This is a significant correction to make, since Scudder called particular attention to the supposed fact that fossil species of Inocellia were much more numerous than those of Raphidia, the reverse being true of the Recent fauna. A glance at Scudder's specimens or at his figures of the fossils shows at once that all of his species of Inocellia possessed the long slender prothorax or the oval head of Raphidia, or some other characteristic which enables instant recognition of the latter genus. Cockerell and Custer (1925) in looking for some feature that might be used to distinguish the wings of the members of these two genera, noted that in Inocellia there was always a cross-vein between Rl and Sc near the end of the latter, and that this cross-vein was invariably absent in Raphidia. In applying this observation to Scudder's species, they noted that the cross-vein was present in at least two of Scudder's species of Inocellia (*tumulata* and *veterana*), although these

fossils are typical members of Raphidia in other respects. The explanation of this apparent contradiction of characters has finally come to light with the discovery of a specimen of snake-fly from the Creede (Miocene) shales of Colorado; this specimen is a splendid one showing all wings as well as the body structure clearly. A study of this specimen shows that although the cross-vein at the end of Sc is present in one fore wing, it is entirely absent in the other! Thus it appears that in spite of the fact that the absence or presence of this cross-vein is a very reliable difference between the *living* species of the two genera, it cannot be used in the Tertiary species because it had not become stable in the Raphidiidæ. This of course explains why some of the specimens typical of Raphidia described by Scudder (as belonging to Inocellia) possess this cross-vein.

Family Raphidiidæ

Since the genera of this family are distinguished only by the structure of MA in the hind wing (aside from the genitalia), it is necessary that at least a part of the hind wing be preserved in the fossil specimens for accurate determination. Fortunately, the hind wing is partially preserved in several of the type specimens, and when the probable synonomy of the fossils is taken into account, a good proportion of the species can be placed accurately in genera. In 1910 Handlirsch, in rearranging the classification of the fossil snake-flies, established two new genera for Scudder's species: Dictyoraphidia for *veterana*, and Archiraphidia for *tumulata*, *tranquilla*, and *eventa; somnolenta* he left in Inocellia with some doubt. Handlirsch, however, did not see Scudder's specimens, and his conclusions were based upon assumptions which are not valid, and his genera based upon venational characteristics which appear in any series of specimens of Recent Raphidia. Cockerell placed one species, *elegans*, in a distinct genus, Megaraphidia, but, as he later pointed out (1908, p. 342), the characteristics of that genus are approached in some specimens of Raphidia, suggesting that possibly Megaraphidia should be reduced to a subgenus. Unfortunately the type of this species has been either lost or destroyed. A fragment of shale bearing this name and marked "type" was sent to me by Dr. C. A. Reeds of the American Museum of Natural History; but there were no remains of an insect discernible. That the type of this particular insect is lost is most regrettable, but with the corrections indicated by Cockerell (Rohwer, 1909, footnote p. 534), there is nothing to eliminate this wing from either Raphidia or

Agulla and in view of the generic position of the other Florissant species it is assigned here tentatively to Raphidia.*

Eventa was not figured by Scudder, but an examination of the two types shows that part of the hind wing is present in both specimens and that *MA arises at the base of the wing*, which places the insect in Raphidia. The hind wing of *pulveris* Cockerell has already been described by Professor Cockerell from a single, splendidly preserved wing; this hind wing belongs almost certainly to that species. In this specimen MA also originates at the base of the wing, as in Raphidia. Part of the hind wing is well preserved in the type of *mortua* Rohwer; and in this we likewise find that MA arises as in Raphidia. Although these are the only specimens of hind wings of the Raphidiidæ which have thus far been known, it is pertinent to note that in the new species (*creedei*) from the Miocene shales of Creede, described below, MA is again identical with that of Raphidia. Since there is no evidence to the contrary, it seems very probable that the other fossil Raphidiidæ described from the Florissant shales belong to Raphidia and they have been so placed in this paper.

With the wings as the only source of characteristics, it is very difficult to arrive at a satisfactory species taxonomy, especially in the Raphidiodea. Professor Cockerell experienced this many years ago and stated (1914, p. 715) that, "Modern species of Raphidia show so much variation in the venation, even on the two sides of the same animal, that fossil species distinguished by the structure of the wings must be regarded as more or less provisional. Possibly the material will never be sufficient to decide definitely whether we have too many or too few specific names." There are, however, certain structures of the wings which can be used for species classification in the absence of better characteristics. The shape of the pterostigma and the size and shape of the wings are fairly constant within certain limits in the Recent Raphidiodea, and will certainly be more satisfactory than the obviously useless venational details, such as have been employed in the past. It is already clear that too many species of fossil Raphidiidæ have already been described from the Florissant shales. Of the ten species of snake-flies which have been described

* After this paper had been sent to the press, the reverse of the type of *M. elegans* was found in the University of Colorado Museum, and was loaned to me for study. There is nothing showing in the fossil (almost a complete fore wing) which eliminates the insect from Raphidia. It may be identical with *R. exhumata*, but in view of the larger size of *elegans* it seems advisable to consider the species as distinct.

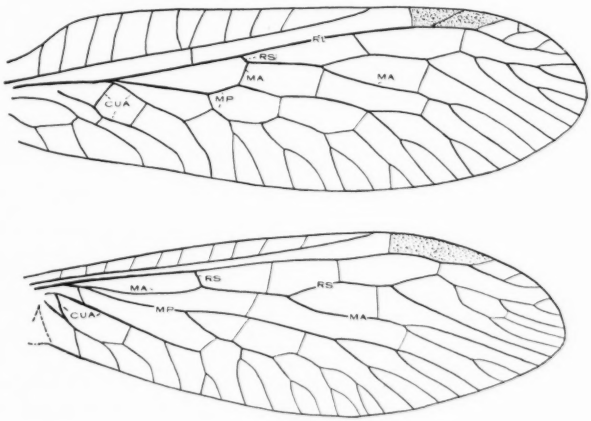
from the Florissant shales, seven are known only from uniques, and the remaining three by two specimens each. The chances of obtaining seven distinct species of the same genus or family in a collection of seven specimens from one locality are too remote to be considered. Unless some attempt is made to classify the specimens on the basis of characteristics which have some specific value in the Recent members of the group, the number of species will increase indefinitely (like Navas' genera) as long as additional specimens are obtained. In the following account I have therefore synonymized certain species on the basis of the similarity of the pterostigma and size.

Genus *Raphidia* Linn.

Raphidia exhumata Cockerell

Text-figure 9

Raphidia exhumata Cockerell, 1909, Bull. Amer. Mus. Nat. Hist., 26, p. 73. Cockerell, 1912, Ent. News, 23, p. 215.
Raphidia pulveris Cockerell, 1914, Journ. Geol., 22, p. 714.



TEXT-FIGURE 9. Fore and hind wings of *Raphidia exhumata* Cock., from the Miocene of Florissant, Colorado. Fore wing drawn from type.

Fore wing: length, 11–12.8 mm.; width, 3.5–4 mm. Costal space broadened as much as in *R. ophiopsis;* pterostigma short, about 4½

times as long as wide; venation typical of the genus, without any unusual features other than those obviously individual. Hind wing: length, 10 mm.; width, 3 mm.; pterostigma shaped as in fore wing.

Body unknown.

Holotype.—Florissant (Miocene) Colorado, Sta. 13B, 1908 (S. A. Rohwer); in the University of Colorado Museum.

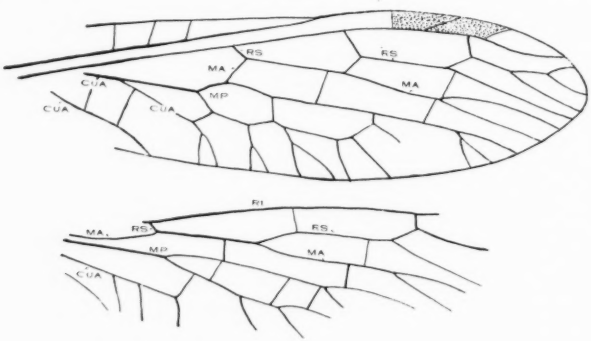
The wings of this insect show no differences whatever from those of the Recent species of Raphidia. An examination of the types of both *exhumata* and *pulveris* convinces me that these species are synonymous. Unfortunately each type consists only of a fore wing, but a hind wing (text-fig. 9), already identified by Cockerell as *pulveris*, almost certainly belongs to this insect. The free proximal part of MA in the hind wing is clearly preserved, and furnishes the key to the genus.

Raphidia mortua Rohwer

Text-figure 10

Raphidia mortua Rohwer, 1909, Amer. Jr. Sci., 28, p. 533.

Fore wing: length, 10 mm.; width, 3 mm. Costal area not broadened as much as in *exhumata;* pterostigma long and narrow, at least 7 times



TEXT-FIGURE 10. Fore wing and part of hind wing of *Raphidia mortua* Rohwer, from the Miocene of Florissant, Colorado; drawn from type.

as long as broad. Hind wing incompletely preserved, but showing the free proximal piece of MA very well.

Holotype.—Florissant (Miocene), Colorado; Sta. 14, 1908 (G. N. Rohwer); in the University of Colorado Museum. The type consists

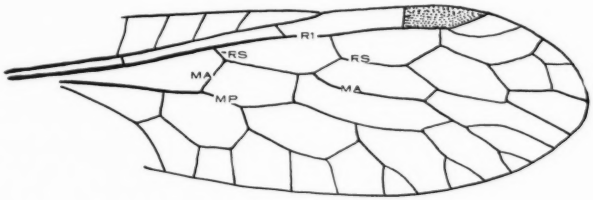
of a fore wing, part of a hind wing, the abdomen, and the thorax except for the prothorax.

The species differs from the foregoing by the more slender wing and the elongate pterostigma. The hind wing is partially concealed by the fore wing, but enough of it can be distinguished to enable the generic determination to be certain.

Raphidia tumulata (Scudder)

Text-figure 11

Inocellia tumulata Scudder, 1890, Tert. Ins. N. A., p. 158; pl. 14, fig. 15.
Archiraphidia tumulata Handlirsch, 1910, Contr. Can. Pal., 2, p. 103.
Inocellia eventa Scudder, 1890, Tert. Ins. N. A., p. 160.
Archiraphidia eventa Handlirsch, 1910, Contr. Can. Pal., 2, p. 103.



TEXT-FIGURE 11. Part of fore wing of *Raphidia tumulata* (Scudder), from the Miocene of Florissant, Colorado; drawn from type.

Fore wing: length, 9 mm.; width, 2.7 mm.; costal area not quite so wide as in *exhumata;* pterostigma very short, only about twice as long as wide. Hind wing: length, 7.8 mm. Length of whole body about 12 mm.

Holotype.—Florissant (Miocene), Colorado; in Museum of Comparative Zoology (No. 244).

The pterostigma of this insect is far shorter than in any of the other fossil species. The type specimen, which is obviously a male, shows the oval head and elongate prothorax characteristic of the Raphidiidæ. The head in the type is 1.8 mm. long, and .8 mm. wide; the prothorax 2 mm. long and .4 mm. wide.[21] *Eventa* was not figured by Scudder, though both type specimens, which are in the Museum of Comparative Zoology, are very well preserved. An examination of these convinces me that the species is identical with *tumulata*, the

[21] Scudder gave the length of this prothorax as 1.6 mm., but this is incorrect.

pterostigma being similarly shaped. One of the types of *eventa* (M. C. Z., No. 253; Scudder's No. 8319) includes portions of the body, and is obviously a male. The head is 2.2 mm. long and 1 mm. wide. The prothorax is 2.4 mm. long and .5 mm. wide. The shape of the head, length of the prothorax, and the veinlets bordering the pterostigma of all three specimens are conclusive evidence that this species belongs to the Raphidiidæ.

Raphidia tranquilla Scudder

Raphidia (?) *tranquilla* Scudder, 1890, Tert. Ins. N. A., p. 154; pl. 14, fig. 2.

Inocellia somnolenta Scudder, 1890, Tert. Ins. N. A., p. 157; pl. 14, fig. 12.

Archiraphidia tranquilla Handlirsch, 1910, Contr. Can. Pal., 2, p. 103.

Fore wing: length, 7.75 mm.; width, 2.5 mm.; costal area apparently not very broad; pterostigma short, about 4½ times as long as wide. Hind wing unknown.

Holotype.—Florissant (Miocene), Colorado; in Museum of Comparative Zoology (No. 246).

This is the only species of the Florissant Raphidiidæ of which the hind wing is entirely unknown. In view of the fact that all the other fossil Raphidiidæ of the beds belong to Raphidia, I have placed this species there also, there being no evidence to the contrary. The type specimen of *tranquilla* is very poorly preserved, the wings being overlapped in such a way that it is very difficult to make out the venation of a single wing. Scudder's figure, which attempts to reproduce the venation of a fore wing, is certainly incorrect in so far as the pterostigmal region is concerned. By placing Canada balsam on the specimen, I succeeded in obtaining a good view of this part of the wing; and the pterostigma turns out to be very much like that of *somnolenta*. The latter does not show the venation well either, because of the overlapped wings; but there is no reason for regarding these two species as distinct. For some reason not at all clear Scudder concluded that the type of *somnolenta* was a female; there is, however, no sign of an ovipositor in the specimen, nor is it mentioned in Scudder's description or included in his figure.

Raphidia creedei, n. sp.

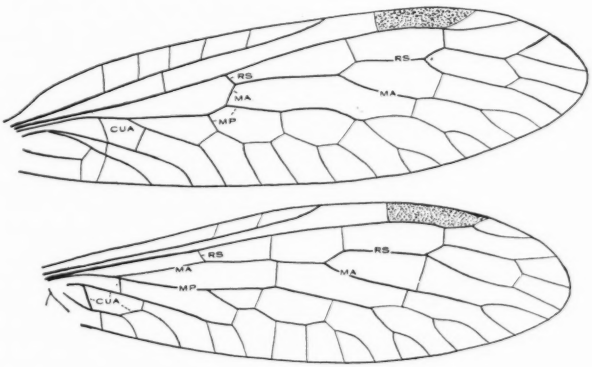
Text-figure 12

Fore wing: length, 9 mm.; width, 2.5 mm.; costal space unusually narrow; pterostigma rather short, about 4 times as long as broad;

venation typical of the genus, with no specific peculiarities. Hind wing: length, 8 mm.; width, 2.2 mm. Length of body (excluding head and ovipositor), 11 mm.; prothorax slender, 2.5 mm. long and .8 mm. wide; rest of thorax 2.5 mm. long; abdomen 6 mm. long.

Holotype.—Creede shales (Miocene), near Creede, Colorado; collected in 1934 by Mr. Allan Caplan, a member of the writer's collecting party.

The specimen on which this species is based is one of the most com-



TEXT-FIGURE 12. Fore and hind wings of *Raphidia creedei*, n. sp., from the Miocene of Creede, Colorado; drawn from type, No. 3639ab, Museum of Comparative Zoology.

plete and satisfactorily preserved fossil snake-flies; and it is the only female among the numerous New World fossils of this group. The insect as preserved shows a dorsal view. Both right wings are well preserved and not overlapped; the left wings, although lying together, are placed in such a way that it has been easy to work out certain details in the proximal part of the hind wing not so clear in the right wing. Most of the head is missing, the front part of the prothorax being almost at the edge of the piece of shale. The prothorax is 2.5 mm. long and .8 mm. wide; the rest of the thorax 2.5 mm. long. The abdomen is 6 mm. long, and the ovipositor projects about 3 mm. beyond the abdomen. That the ovipositor was originally curved like that of Recent snake-flies is indicated by the recurved apex.

This insect is the third to be described from the Miocene shales at

Creede.[22] It differs from all the Florissant species by the more slender wings and the very narrow costal area of the fore wings.

Family Inocelliidæ

Genus *Fibla* Navas

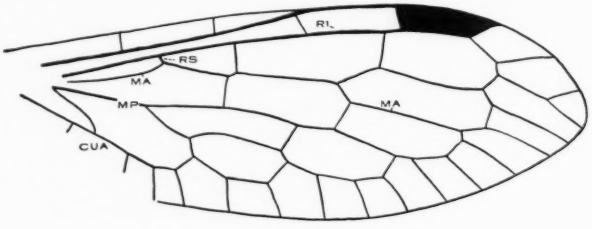
Fibla Navas, 1915, Mem. R. Acad. Cienc. Art., 11, p. 477.
Burcha Navas, 1915, Mem. R. Acad. Cienc. Art., 11, p. 478.

Fibla exusta (Cockerell and Custer)

Text-figure 13

Inocellia exusta Cockerell and Custer, 1925, Ent., 58, p. 295; figure.

Hind wing: length 8.5 mm.; 3.2 mm. wide; costal space narrow, as in the hind wings of Recent Inocelliids; pterostigma 4½ times as long as wide, very dark; MA coalesces with Rs at a point closer to the origin



Text-figure 13. Hind wing of *Fibla exusta* Cock. & Custer, from the Miocene of Florissant, Colorado; drawn from type.

of the latter than is usually the case, but that is probably an individual variation; cross-vein between M and Cu long and slightly sigmoidal, as is characteristic of the family.

Holotype.—Florissant, Colorado; S. A. Rohwer; in University of Colorado Museum. The type consists of a splendidly preserved hind wing.

That this fossil belongs to the family Inocelliidæ is proven by the dark, unbordered pterostigma and the oblique cross-vein between M and Cu in the proximal part of the wing. Its generic position is shown, of course, by the basal origin of MA. It is exceedingly for-

[22] A detailed account of the insect-fauna of these newly discovered beds is now in preparation. It has, however, seemed advisable to describe this snake-fly in this revision, rather than wait until the former paper has been completed.

tunate that this fossil Inocellid consists of a hind wing rather than a fore wing, for the latter would not have contained the necessary generic features. The present species, the sole fossil representative of the family Inocelliid in North America, is beyond question a member of the genus Fibla, which like Raphidia, is now confined to a part of the Old World.

Affinities of the Nearctic Snake-fly Fauna

The generic relationships exhibited by both the extant and extinct Nearctic Raphidiodea appear to throw some light on the origin of this particular fauna. The affinities between the American species and those of other continents have in the past been much obscured by Navas' artificial generic classification; but they have been clarified by the new classification, which in my opinion places the systematics of these insects on a basis of their true phylogeny.

As I have already mentioned, the oldest fossil snake-flies, from the Jurassic of Turkestan, possess an anterior media (MA) in the hind wing like that of the genera Raphidia and Fibla (as defined above); that is, the vein diverges from the stem of M close to the base of the wing, and after running parallel to the longitudinal axis of the wing for some distance, finally coalesces with the radial sector. The body structure of these ancient snake-flies differs from that of the Recent ones in having a shorter prothorax; and the venation differs in several respects, but chiefly in having the radial sector arising nearer to the base of the wing. After the Jurassic the next record of these insects is in the Oligocene Baltic amber. A single species has been described from this formation, *Inocellia erigena* Hagen. The wings of Hagen's specimen were not very clear, and his figure shows that he was unable to make out satisfactory the course of several veins. The body structure, however, was well preserved and it is at once apparent from Hagen's figure that the species has all the body characteristics, including the lack of ocelli, of the Inocelliidæ. It is obvious, therefore, that by the time of the Oligocene, at least, the snake-flies already included the two types which are now regarded as families. The generic position of this amber species may perhaps be open to some question until more satisfactorily preserved specimens have been secured, but it is clear from the venation of the left hind wing of Hagen's figure that the insect has the characteristic of Fibla—the anterior media (MA) arises at the base of the wing. This is a particularly interesting point because when we consider also the Miocene fossils, we find that all the Tertiary Raphidiodea known belong to the

genera Raphidia and Fibla. Whether or not we are justified in concluding from this that the genera Agulla and Inocellia arose since the Miocene is perhaps open to question. The evidence for this is purely negative, but it does fit in perfectly with the concept that, as indicated by the more specialized nature of MA in the hind wing, Agulla and Inocellia are more highly specialized than Raphidia and Fibla. It is also consistent with the geological history of other groups of Neuropteroid insects; for as I have previously pointed out, both the Mecoptera and Chrysopidæ have evolved so much since the Miocene that not a single Tertiary fossil is referable to a Recent genus. In the case of the Raphidiodea, it seems evident that while new genera have been evolved since the Miocene, at least two of the Tertiary genera (Raphidia and Fibla) have persisted until the present time.

In view of these geological data, the composition and distribution of the snake-fly fauna in North America is particularly interesting. The two genera which occur in the Miocene of Colorado no longer exist in the New World, but are confined to the Palearctic region, one (Fibla) being restricted to the southern part of Europe. This is strong evidence that the present snake-fly fauna of North America has been newly formed since the Miocene, the Mid-Tertiary fauna having been exterminated.[23] The restriction of the Recent genera in North America to the Rocky Mountain and Californian regions points to the conclusion that the present snake-fly fauna of North America has been derived from eastern Asia through Alaska. This migration could easily have extended southward along the Pacific coast into South America, giving rise to the two isolated species of Agulla which occur in Central America and Chile.

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[23] This conclusion is consistent with the history of several other groups of insects in North America. The tse-tse flies (Glossinidæ) for example, which were a part of the Miocene insect fauna of Colorado, are now restricted to the sub-tropical and tropical regions of the Old World.

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EXPLANATION OF PLATE 1

FIG. 1. *Agulla unicolor*, n. sp.; ventral view of ♂ genital segment; *aed*, aedeagus; *hrp*, harpogon; *prm*, paramere.

FIG. 2. *Agulla neglecta*, n. sp.; ventral view of ♂ genital segment; left harpogon partially removed.

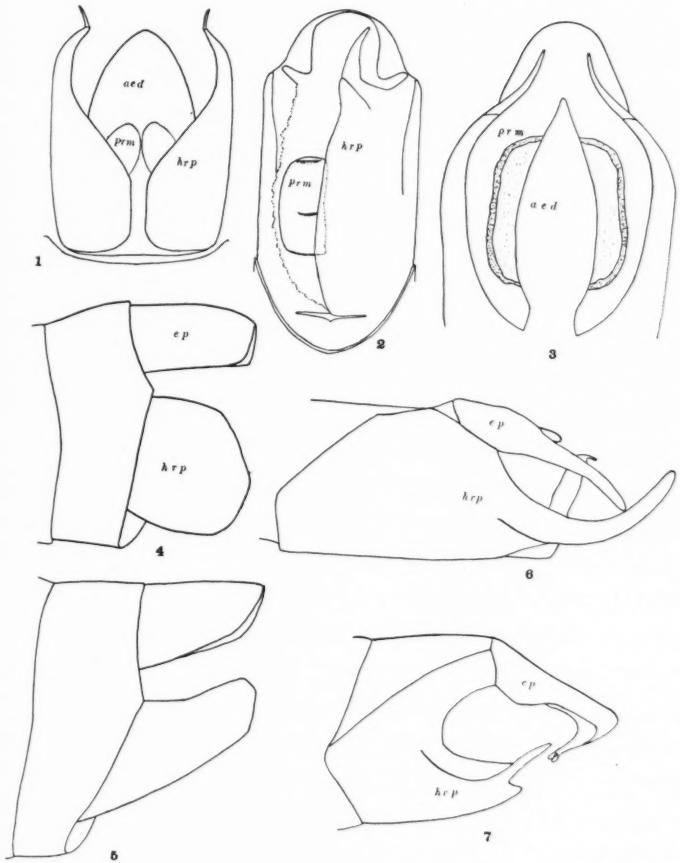
FIG. 3. *Agulla directa*, n. sp.; ventral view of ♂ genital segment; harpogones opened.

FIG. 4. *Inocellia longicornis* Alb.; lateral view of ♂ genital segment; *ep*, epiproct.

FIG. 5. *Inocellia inflata* Hagen; lateral view of ♂ genital segment.

FIG. 6. *Agulla* (*Alena*) *minuta* (Banks); lateral view of ♂ genital segment.

FIG. 7. *Agulla* (*Alena*) *distincta* (Banks); lateral view of ♂ genital segment.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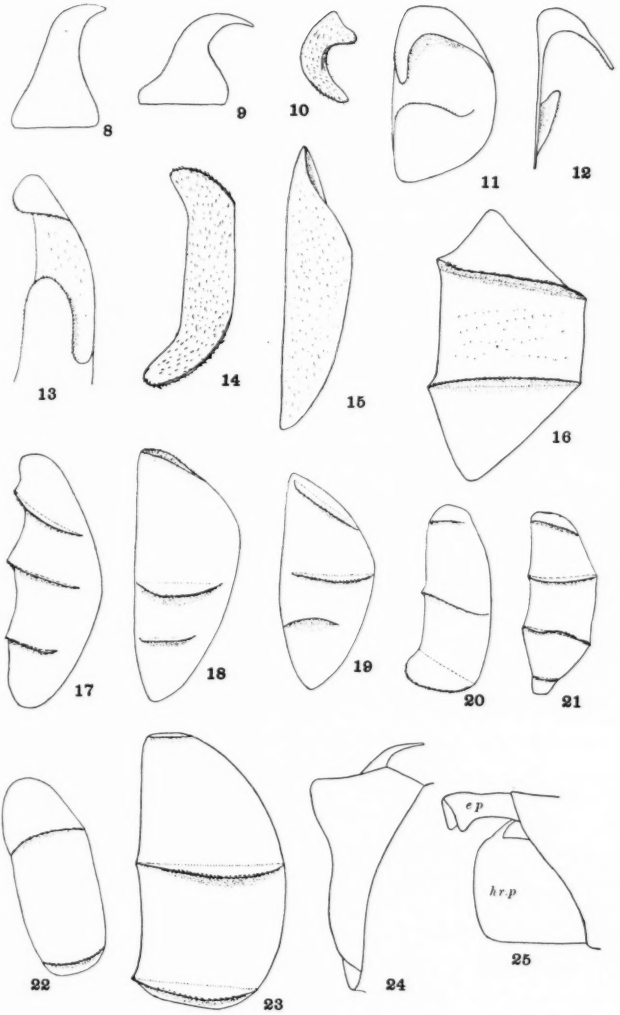
EXPLANATION OF PLATE 2

FIG. 8. *Agulla adnixa* (Hagen), right paramere.
FIG. 9. *Agulla adnixa* (Hagen), right paramere.
FIG. 10. *Agulla flexa*, n. sp., right paramere.
FIG. 11. *Agulla banksi*, n. sp., right paramere, ventral view.
FIG. 12. *Agulla banksi*, n. sp., right paramere, lateral view.
FIG. 13. *Agulla modesta*, n. sp., right paramere.
FIG. 14. *Agulla arizonica* (Banks), right paramere.
FIG. 15. *Agulla crotchi* (Banks), right paramere.
FIG. 16. *Agulla bractea*, n. sp., right paramere.
FIG. 17. *Agulla bifurca* (Banks), right paramere.
FIG. 18. *Agulla assimilis* (Alb.), right paramere.
FIG. 19. *Agulla assimilis* (Alb.), right paramere.
FIG. 20. *Agulla bicolor* (Alb.), right paramere.
FIG. 21. *Agulla occidentis*, n. sp., right paramere.
FIG. 22. *Agulla astuta* (Banks), left paramere.
FIG. 23. *Agulla singularis*, n. sp., right paramere.
FIG. 24. *Agulla flexa*, n. sp., lateral view of right harpogon.
FIG. 25. *Agulla modesta*, n. sp., lateral view of ♂ genital segment.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